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MUTATIONS AND NATURAL SELECTION

PROFESSOR R. RUGGLES GATES
KING'S COLLEGE, UNIVERSITY OF LONDON

SINCE Darwin's time our knowledge of variation has enormously increased, but although the theory of its action has made some important advances, actual observations of natural selection at work remain extremely meager. This is a field, however, in which the final decision regarding the competence of natural selection as an evolutionary factor must rest with the observer and the experimentalist, and there remains the widest divergence of opinion regarding the rôle actually played by natural selection.

Mutations are now generally regarded as furnishing the raw materials on which selection may act with more or less effectiveness. Such mutations are recognized as large or small, repetitive, often parallel, and apparently for the most part non-adaptive. The question of the effectiveness of natural selection in sifting out these variations is one of great importance.

In his important work, "The Genetical Theory of Natural Selection," Fisher (1930) has made a mathematical analysis of the action of natural selection to which brief reference may be made. He shows that population-size, *i.e.,* the number of intercrossing individuals in a species, has an important bearing on the conservation of variance, and that the chance of survival of a particular gene in a species is represented by the coefficients of a Poisson series. He further shows (p. 77) that while a selective advantage of the order of 1 per cent. is ample to bring about evolutionary change in a species having a

population of 1,000,000, it scarcely differs in effect from random or chance survival when only a few individuals are in question.

Now if I understand him correctly, the basis of this mathematical analysis is the assumption that the individuals of a species, even if they extend over a continent and number 100,000,000 or more, are not only all equally capable of producing a particular mutation but are also all really in a position to interbreed. The latter is, however, clearly not the case with any widely distributed species, and this appears to weaken his argument regarding the incidence of natural selection. Each species must have an effective average range of interbreeding and dispersal of individuals which is very much less than the whole geographical range of the species, except in species of relatively narrow range and small numbers. To the latter, Fisher agrees that his formula would not apply. Of course, it is admitted that if natural selection is favoring a gene it will gradually spread from its center of origin into other areas. But if natural selection is not at work, then the only effective competitors against spread will be those relatively few individuals in its immediate neighborhood.

This distinction between the effective intercrossing range, which appears usually to be quite narrow, and the geographic range of the species, appears to me to be important. Among even the most widely ranging quadrupeds, the wanderings of the individual will represent usually but a very small fraction of the species range, and its possible mates will, as a rule, not be numbered in millions or even in thousands. Can the Poisson series then be applied to them? Even migratory birds of many species return each year to the same locality, and their effective mating possibilities are limited accordingly. Indeed, it is, I think, generally agreed that geographic races can only develop under conditions of isolation in so far as interbreeding is concerned. The effective population to which the Poisson series can be applied appears therefore to be not the whole species, nor even necessarily the

whole range of a geographic race, but simply the average number of individuals with which a member of that species has the actual (as contrasted with the theoretical) possibility of mating.

In the case of plants, what I may call the effective intercrossing population, in contrast to the whole population of the species, will be greatly limited by the fact that they are (1) stationary and (2) usually hermaphrodite. On the other hand, it will be extended by the visiting ranges of particular flower-visiting insects, or in anemophilous plants by the effective range of the wind in carrying pollen.

If these conclusions are correct, then the spread of new genes arising in most species would be determined mainly by chance alone in its earlier stages; but selection might come in later to hasten the spread of certain genes which proved to be advantageous to the species, after they had transgressed the bounds of the effective intercrossing population in which they had arisen. It has to be admitted, however, that so far as plants are concerned, there is, in the great bulk of cases, no evidence whatever that natural selection is aiding the spread of a new form or variety of narrow distribution. In occasional cases, on the contrary, the evidence of selective action seems clear. It may also be pointed out that the higher the mutation rate with which a new non-adaptive gene appears, the better chance it will have of spreading and becoming incorporated with the species over a certain portion of its area. Before discussing this subject further, it will be well to cite a few instances, chiefly from the North American flora. Many others were discussed in a former work (Gates, 1921).

Saxifraga Virginiensis var. *pentadecandra* is an apetalous form in which the five petals are replaced by stamens. It was described in 1887 as "extremely scarce" on Manhattan Island. In 1898 it was reported as "abundant" on slaty rock in Essex County, Massachusetts, being observed at a certain station for several years. The absence of petals may be regarded as a definite disadvan-

tage both as regards protection in the bud and attraction for insects, yet this form was able to survive as a mutation in different areas and become abundant in one. Clearly natural selection was in abeyance so far as it was concerned, at any rate during the period of its successful spread. The European *S. granulata* L. is known to produce the same variation in cultivation. There are also numerous early records of wild double-flowered mutations of *S. Virginiensis*[1] in Massachusetts, New York, Connecticut and Delaware over a quarter-century period from 1849 to 1872. "Doubling" of course produces sterility and must be a very disadvantageous character to the species, yet it occurs wild in innumerable species repeatedly by parallel mutations. Not only do many of these survive, but they may even spread. This was the case with a large patch of *Sagittaria variabilis* having completely double flowers found on the Susquehanna River, which thus showed its capacity to spread vegetatively when sexual reproduction was entirely cut off.

Fernald, a close observer with an unsurpassed knowledge of the Atlantic American flora, has made numerous records which appear to me to have a similar significance. Thus he described near St. John's, Newfoundland, a "considerable colony" of *Kalmia angustifolia* forma *candida* with white flowers, showing that a mutation can spread without the aid of selection. A single specimen was also found at Sherborn, Massachusetts. Such trivial cases are, of course, innumerable, and it might be argued that all such mutations soon reached the end of their tether, when natural selection finally began to act; but there are cases where a wide and successful species shows a similar color difference from its neighbors. Here we may suppose that a useless or even disadvantageous character has spread by chance beyond the effective intercrossing population where it appeared and has become linked with a character on which selection can act.

Another record of some interest, as indicating how muta-

[1] For other variations of Saxifraga see Fernald in *Rhodora*, 19: 141–144. 1917.

tions may be related to natural selection, is that of a dwarf form of *Drosera rotundifolia* which Fernald (1905) found in a sphagnous bog in the Gaspé peninsula, Quebec. The normal species was abundant at the borders of the bog, which was abundantly and almost exclusively occupied by this var. *comosa* in an area of perhaps half an acre. It was dwarf, subcapitate, with few flowers and colored petals. But the ovary, instead of producing normal capsules, "tended to develope into a rosette of glandular foliage-leaves," and the same tendency was shown to a less extent in other floral organs. Whether or not all these differences were the expression of a single mutation, this form had succeeded and spread in an extreme habitat where it reproduced vegetatively and the species was evidently at a disadvantage. The dwarf form appears to have been better adapted than the type to the conditions in or near which it happened to arise, and selection has therefore favored it. A parallel form with leaf-like carpels has been described and figured by Planchon (1848) in the European *D. intermedia.* The fact that such a condition is teratological does not lessen its interest in relation to natural selection.

In a discussion of the mutation theory and the species concept (Gates, 1917), many facts of geographic variation in plants and animals were considered. One particularly pertinent case may be referred to here. *Maianthemum canadense,* which is widely distributed in North America, is glabrous throughout the greater part of its range, but a heavily hirsute var. *interius* Fern. occurs in the arid region of the Black Hills of South Dakota, near the western extremity of the range of the species. In Minnesota and Wisconsin a semi-pubescent form occurs. It appears that the hirsute variety is a mutation, perhaps from the semi-pubescent form, which enables the species to extend its range into an arid area where the glabrous type could not survive.

In a paper on the beginnings of specific differentiation in plants, Fernald (1934) has cited a number of examples, one of which may be referred to here. *Epilobium glan-*

dulosum is widely distributed in North America, and on the great estuarine tidal flats of the St. Lawrence it has produced a form—*E. ecomosum* Fern.—which differs in (1) absence of the coma on the seeds, which distinguishes the genus Epilobium from Oenothera and other genera, (2) seeds gray and covered with ridges of coarse papillae, while in *E. glandulosum* they are brown and only minutely pebbled. The fact that these seed characters have been altered while the rest of the plant remains essentially unchanged notwithstanding its very special habitat, with diurnal submersion and emersion, suggests that the changes have been produced by two or three mutations. Crossing experiments with these two species would be of great interest.

Again, consider the case of *Silene antirrhina* L., in which Fernald described a form which is entirely glabrous, *i.e.*, the glutinous band found on some internodes of the type is absent. That such bands are of no use to the plant, as a flypaper for insects or otherwise, is indicated by the fact that the glabrous form is occasional throughout the range of the species and is constant in the colonies where it occurs. The distribution of this form seems to be determined solely by its spread to form colonies in the various locations where it has arisen as a mutation from the type.

Finally, as representing a somewhat different class of case, *Betula nana* L. var. *Michauxii,* of Newfoundland and adjacent portions of Canada, differs from the type in having the bracts of the female catkins simple (not three-lobed), and Fernald has described from Mt. Albert, Gaspé, *B. alba* L. var. *elobata,* which differs from the species in the same respect. These are evidently parallel mutations which have no selective value whatever, either positive or negative, and they are typical of innumerable characters differentiating plant species. One must conclude that the origin of all such characters has taken place without any interference from natural selection. But there are various rôles that selection may come to play in their later history. That the differentiation of a whole

series of species may take place with the minimum of interference from natural selection is indicated in the genus Antirrhinum, where Baur found the various European species to be distinguished only by simple Mendelian characters.

Kristofferson (1926) has intercrossed seven species of Malva and he finds that all the specific characters show Mendelian segregation. Several independent factors were recognized, while such characters as flower-size and number of carpels showed multifactorial segregation. *M. parviflora* L. and *M. oxyloba* Boiss. form an interesting pair of species, the latter having sharply serrate leaves and long-pointed sepals, the former crenate leaves and short-pointed sepals. *M. parviflora* is also taller, with thicker stem and heavier fruits, these differences probably resulting from the greater leaf surface for assimilation. In crosses, all these differences behave as a single unit, with the leaf and sepal characters of *M. oxyloba* almost completely dominant, but there was also some evidence of modifying factors. One plant of *M. oxyloba* gave a chimeral reversion of one branch to *M. parviflora*. The distribution of these species is interesting, *M. parviflora* being found throughout most of Europe, from India to Palestine and Cyprus, and across northern Africa to the Canaries; while *M. oxyloba* is known only from Cyprus, Palestine and Syria. Is *M. parviflora* the parent type which has given rise to the weaker *M. oxyloba* through a dominant mutation, or has *M. oxyloba* produced the stronger and more successful *M. parviflora?* In either case *M. oxyloba* has been able to cover quite a wide area in spite of natural selection obviously favoring its stronger rival.

The modern cytogenetic work shows that in many cases new genera, sub-genera and species have been produced as the result of tetraploidy, amphidiploidy, chromosome duplication, fragmentation, segmental interchange and similar chromosome changes. Natural selection has had no part in the production of these internal structural changes, which are sufficiently accounted for by the na-

ture of the cell mechanisms involved. But natural selection may aid in the spread of such a new form once it has appeared, as in the case of the amphidiploid *Spartina Townsendii* which spreads rapidly because of its great vigor.

Hagerup (1933) has brought evidence to show that various tetraploid and higher polyploid species of plants are adapted to more extreme conditions, both in the arctic and in the Sahara, than their diploid relatives. Tischler finds that at least 44 per cent. of the Angiospermum species in the flora of Schleswig-Holstein whose chromosome numbers have been determined are polyploid. Rohweder (1936), in a recent further study of this flora, finds that the presence of lime in the soil-water exercises a selective action as between diploids and polyploids. In dry turf, and especially in the sand and heath on old moraines, in soils containing little chalk, diploid species largely predominate; whereas in the flora of the ditches of the Elbe marshes, where the lime content is high, as many as 95 per cent. of the common species may be polyploid. Similarly, in areas of Flachmoor, where the soil contains considerable lime, the polyploid species are estimated at 79 per cent. In all such cases it seems clear that selection does not foster the origin of polyploids, but aids their spread in areas where the environmental conditions happen to favor them against their diploid rivals. In other areas it will equally favor the diploids.

The conception of parallel mutations was first announced in connection with Oenothera (Gates, 1912). Such parallels are a corollary of the mutation theory and they are found everywhere in the plant and animal kingdoms, many of them as single characters, many others as shorter or longer parallel series. A large volume would be required even to enumerate them, but we may select a few from various plant and animal groups, as the question of parallelism in general has a fundamental bearing on the incidence of natural selection. Many cases were considered in "Mutations and Evolution" (1921); Vavilov (1922) cited numerous homologous series of variations

in Gramineae, Cucurbitaceae, Papilionaceae and other families. Matsuura (1935) emphasizes the importance of genotypic parallelism as a basis of group variability.

Parallel characters are conspicuous in the Cyanophyceae, where the morphological possibilities are at a minimum, but where, in the absence of sexuality, they could not be transferred from species to species by hybridization. It is now well recognized that the group of Chlorophyceae (in the widest sense) are shot through with parallelisms which involve both morphological and physiological characters. Every student of the Liverworts recognizes much parallel development in this group. Apart from the development of such specializations as water pitchers, paraphylls, coelocauly and marsupia, in different groups, the evidence seems clear (Gates, 1931) that elaters, with their beautiful hygroscopic spirals, have developed several times independently, not only in the Liverworts but also in the Mycetozoa. Here, if anywhere, natural selection may be expected to have played a rôle, as these cell structures are clearly adaptational, but the evidence for it is at present purely conjectural, and all stages in the "perfecting" of these structures are found in different species of the group.

The nature of the numerous long, parallel phyletic lines emphasized by Bower (1928) in the ferns and extending over several geological epochs is open to various interpretations and need not be considered here, except to say that it involves many more things besides parallel mutations.

The shifting cross-relationships recognized in the taxonomy of innumerable families of flowering plants and emphasized by Hayata (1920) must be mainly accounted for by the recognition of a large amount of parallel variation, although some of this may have arisen through the transfer of characters by crossing. In very few instances, either in plants or animals, has it been shown genetically that these parallelisms are due to the same gene in related species, and yet the cumulative evidence points very strongly to this conclusion, and everything

we know of the structure of the germplasm tends to confirm it.

With animals, the longer parallel series appear to be concerned usually with adaptation to different media or habitats, and hence presumably with natural selection, as in the case of various groups which have taken to the water or to the air. But, as pointed out by Robson and Richards (1936), this explanation can not always be applied, for the Edentata and the Cetacea show a number of striking parallelisms of specialization, although adapted to wholly different conditions. Here the same parallel series of variations appear to have occurred independently, and if they were regarded as aquatic adaptations in the whales it would be impossible to regard them also as adaptations to a terrestrial insectivorous life in the Edentata. Hence it seems impossible to suppose that natural selection had any part in their production. Parallelisms were well known to Darwin, who called them "analogous variations." Where he used the phrase "the tendency to vary" we may speak in modern phraseology of the capacity of the germplasm to produce parallel mutations in successive series, and this appears to be as near to an explanation as we have yet arrived.

The human blood-groups appear to be a case where the spread of non-adaptive characters has taken place through heredity and migration, in the absence of selection. This problem has recently been discussed elsewhere (Gates, 1936).

Le Gros Clark (1936) has recently pointed out numerous extensive parallelisms in human phylogeny. He refers to parallelisms between (1) lemurs and monkeys, (2) within the Lemuroidea, (3) between Tarsioids and Anthropoids, (4) Old and New World Monkeys, (5) Man and gorilla, (6) the Chancelade and Eskimo skulls, (7) Eoanthropus and Sinanthropus. While some of these parallelisms have apparently been guided in their development by natural selection, many others can lay no such claim. He emphasizes that the mere consideration of resemblance may lead to error regarding relationships.

Bather (1920, 1927) has discussed the subject funda-

mentally from the paleontological point of view. He shows how abundant are parallel synchronous changes in the phylogeny of animal groups traced through successive strata; and he makes it clear that in many parallel lineages the species of one grade or at one paleontological level all pass into another grade or genus at the next higher level. Whatever the full explanation of these wide-spread phenomena may be, it seems that they are made possible in the first instance by the fact that the germplasm of a contemporaneous series of related species possesses in each case the capacity for producing the same mutation—a condition which is equally characteristic of modern living species.

Calman (1935), in a discussion of the meaning of biological classification, considers the conclusions of Bather and others, and while admitting a great amount of parallelism or "convergence," yet concludes that the results of taxonomic research are inconsistent with the view that convergent evolution has been the rule. Nevertheless, every one who considers the abundance of modern evidence will be startled by the pervasiveness of parallel variations.

What are the limits of this parallelism? It obviously has limits, or every modern species would go back to a distinct ancestor at the beginning of evolution. The problem has become of fundamental importance. In any case it is necessary to modify the classical conception of the phylogeny of any group as symbolized by a branching tree whose youngest twigs represent the living species. The phylogeny of most groups appears to be more like the tropical strangling figs, with numerous parallel aerial roots growing out from the branches and frequently coalescing with other branches or with each other.

Finally, it may be said that while natural selection has probably played an important part in connection with some of the longer parallel series, it can not have been a factor in all. And as regards the innumerable parallel mutations in modern species; while a few of them have spread because their differential character was adaptive to a peculiar habitat, the bulk of them have been able

to spread, at least to colonies of considerable size, in the absence of any aid from natural selection. Yet the innumerable parallel characters in the classification of any group indicate that these parallel mutations have played their part in phylogeny.

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ON THE MEANING AND LIMITS OF IRREVERSIBILITY OF EVOLUTION[1]

DR. WILLIAM K. GREGORY
AMERICAN MUSEUM OF NATURAL HISTORY

I. IRREVERSIBILITY AS UNDERSTOOD BY DOLLO

THE Law of Irreversibility of Evolution was first promulgated in 1890 by the late Louis Dollo, of the Musée Royale d'Histoire Naturelle of Belgium, and was developed by him in various later papers, especially in 1890, 1892, 1893, 1905, 1922. It was named Dollo's Law by his distinguished pupil and chief exponent, Othenio Abel, of Vienna. According to Dollo the irreversibility of evolution is due to the irrevocability of the past. He held that when in the course of evolution an organ or a part is lost, that same organ or part is never regained, although a substitute for it may be found if the need arises. Heredity and variation, he said, are unceasing and opposing forces. If, after an organ had disappeared, heredity alone were to continue, the organ might conceivably reappear; but since variation is always operative to a greater or less extent, a complete return to an earlier stage is impossible. So-called "reversions," as in the case of modern three-toed horses, did not constitute in Dollo's eyes a real exception to the law of irreversibility, since, as we shall see later, "reversions" may be accounted for in ways not incompatible with irreversibility.

The adaptability of living matter to changing environmental conditions or to changing opportunities was to Dollo axiomatic. But his theory of irreversibility will work just as well if we accept the theory of preadaptation as advocated independently by Cuénot and Davenport, which is that structural changes in evolution take place

[1] Read at the Tercentenary Conference of Arts and Sciences at Harvard University, September 10, 1936.

solely through mutations initiated in the germ-plasm, and that when an organism finds itself in possession of a new character there is an unconscious selection whereby that new character may either contribute to the extinction of the organism or be fitted advantageously into its life habits. Given the power of adaptation, however achieved, Dollo held that, owing to the irreversibility of evolution, any structure contains in itself a record of its remote past, which can often be read by comparison with others of like kind. In other words, nature has left more or less clearly decipherable records of her experiments, so that each organism is in a sense the summation of all that has gone before.

Accepting irreversibility as axiomatic, in 1913 I proposed to use the word *habitus* for the sum of the more recent adaptive characters by which a given animal is adapted to its present special life habits, and *heritage* for the sum of those characters which have been held over from an earlier set of life habits. Habitus and heritage are correlative terms. Owing to the irreversibility of evolution, the habitus of a remote ancestor becomes part of the heritage of its diversified descendants. When a similar habitus is evolved by animals of diverse ordinal heritage, we have what is commonly called convergence; when a similar habitus is evolved between members of different families of the same ordinal heritage, we have parallelism.

To Dollo paleontological data were treated from the combined viewpoints of paleontology and comparative anatomy, and he would have clearly recognized the myopic futility of the doctrine that in all matters relating either to phylogeny or to the derivation of existing structural patterns, paleontology is the sole court of last resort. For it was by a synthesis of evidence from comparative anatomy, paleontology and taxonomy that Dollo was able to decipher the meaning of many strange structural patterns, such as that presented by the foot of *Diprotodon*.

Diprotodon was a gigantic extinct herbivorous mammal of the Pleistocene of Australia. Its cheek teeth each bore two transverse crests, and to that extent they appear to be similar to those of the extinct proboscidean *Dinotherium*. But *Diprotodon* was eventually proved to be not a proboscidean but a member of the diprotodont marsupials, its nearest existing relatives being the tree-living phalangers and the ground-living kangaroos and wombats. At this point Dollo extended to *Diprotodon* Huxley's hypothesis that all the diverse existing diprotodont marsupials, although now living either on the ground or in the trees, have been derived eventually from tree-living forms not unlike the existing phalangers. The latter have a strange type of hind foot, which is adapted for a double service: the long fourth and fifth digits and the divergent first digit, acting in conjunction with the large friction pads on the sole of the foot, serve as a clamp or climbing organ; the small second and third digits are said to be syndactylous, because they are so closely appressed as to be enclosed in a common web of skin extending to the base of the nails; together they serve as a comb or scratcher for cleaning the fur.

In the light of these and other similar considerations, Dollo analyzed the strange structural characters of the foot of *Diprotodon* as being due to a mixture of old and new adaptations. The foot as a whole retained the fundamental features of the primitive arboreal diprotodont foot, namely, the predominance of the outer side of the foot, the sharp divergence of the hallux and the relatively small size and subequality of the second and third digits. The ancestors of *Diprotodon,* however, after coming down out of the trees, had used their syndactylous hind feet partly for scratching, partly for scraping the ground and partly for the support of the rapidly increasing body weight. Since it was important for the foot to retain mobility as well as to support great weight, the initial turning in of the soles of the foot was preserved and the

bones on the outer side of the foot became enlarged to support the weight, while the small digits on the inner side of the foot were still used in scratching and scraping in a manner remotely analogous to that adopted by the ground sloths.

If time permitted I could cite many similar cases in which the application of Dollo's method to the evidence from comparative anatomy and paleontology enabled him and others to decipher the history of complex morphological patterns, such as the pelvis of dinosaurs, the plastron of marine chelonians, the paddles of ichthyosaurs, plesiosaurs and cetaceans, and so forth. Invariably the results of such analyses have tended to confirm the general doctrine of irreversibility of evolution.

II. Irreversibility, Polyphyletism and Taxonomic Inflation

The principle of irreversibility now finds itself closely associated with a set of newer postulates and principles, which were at most only in their earlier stages when Dollo first began to publish his studies in this subject. I refer to the contemporary estimates of geologic time, to the principle of polyphyletism and to the principle of parallelism.

As to contemporary estimates of geologic time, I need only refer to the fact that there has been an enormous expansion of our conception of the probable time values of the age of the earth as a whole and of the entire series of fossiliferous rocks. In 1892, for example, the duration of the Tertiary period alone was tentatively estimated by Walcott at three million years; geologists of the present time, however, partly as a result of exact measurements of the residual lead in radioactive rocks, assign a tentative estimate of fifty-five to sixty millions of years for the same period.

It is hardly surprising that the discovery that the Tertiary period is about twenty times as long as it was

formerly supposed to be should be supplemented by the further discovery by mammalogists and paleontologists that there are many times more lines of mammalian descent than were formerly dreamed of. From this it is but a short step to the doctrine of polyphyletism or polyphyly, the favorite theme of the late Henry Fairfield Osborn, which is that the very numerous lines of descent (called by him phyla) run independently far back into geologic time before merging into a remote common ancestry, often conceived by him as of Upper Cretaceous age.

Closely related to polyphyletism is the principle of parallelism, which we also owe in part to Osborn: this is, in brief, that long after the main phyletic lines have separated from their common ancestral stock they may develop identical "aristogenes" or new hereditary adaptive characters.

It will be apparent that the concept of irreversibility when placed in this modern setting has a vastly expanded scope. For example, to Osborn, Gidley and others the old picture of a Family Tree with a graded series of branches, sub-branches, twigs and leaves has tended to change into a vast field of nearly parallel vertical lines, running down independently to the Lower Eocene at least and often to the Upper Cretaceous.

The proponents of these ideas have apparently extended the doctrine of irreversibility to imply that even very remote ancestors of any given type must, in order to be admitted as such, already exhibit unmistakable signs of the characters which are very evident in their descendants. On the other hand, those who are familiar with the phenomenon of transformation or metamorphosis expect a claimant to the more remote ancestry of any given type to be free of the specializations which its descendants acquire. For the latter reason W. D. Matthew (1910) in his excellent study of the fossil rodents of North America regarded the Eocene rodent *Paramys* as ancestral at least

to the group that includes the squirrels and beavers, while Miller and Gidley in their classification of the rodents exclude *Paramys* from such ancestry just because it did not have such specializations.

Another case in which a putative ancestor of Lower Eocene time was expected to foreshadow its supposed modern descendant was that of the ancestry of the bears as conceived by Gidley. One of the most striking characteristics of the upper teeth of modern bears is the marked posterior elongation of the first and second upper molars and the very small size of the last upper premolar. Since Gidley believed that such peculiar specializations would require at least the greater part of the Tertiary period for their elaboration, he sought among the Lower Eocene carnivores for some form which would show at least an early stage in the diminution of the last upper premolar and in the elongation of the first two upper molars. Such characters were evident in the creodont genus *Claenodon,* which also happened to have certain bear-like characters of the forefoot; Gidley therefore suggested that the ancestors of the bears had been distinct from other carnivores since Lower Eocene time and that the family of the bears might have been derived from *Claenodon*-like ancestors of that age. Schlosser and Matthew, on the other hand, held that the small size of the last upper premolar and the elongation of the first and second upper molars were relatively recent specializations, partly of late Tertiary age; that the bears had been derived by transformation from primitive dogs, which differ very widely from modern bears in having large shearing last upper premolars and relatively small upper molars; the same authorities also pointed to the genera *Daphoenus, Hemicyon, Hyaenarctus, Ursavus, Indarctos* and *Helarctos* as forming a structural, though not direct, ancestral series in which one might trace the diminution and degeneration of the great shear tooth into the puny last upper premolar of the bear, and at the same time ob-

serve the progress in the elongation of the crowns of the upper molars. After repeated study of the evidence I do not doubt that Schlosser and Matthew were at least much nearer to the truth than Gidley, and that the peculiar specializations of the dentition of the bears have arisen by a relatively recent transformation rather than by undeviating evolution from a remote Eocene ancestor in which the peculiar specializations of the Ursidae were already foreshadowed.

III. Irreversibility, Undeviating Evolution and Transformation

As to undeviating evolution, I have elsewhere[2] defined this concept as including cases in which the earliest known ancestor already shows a distinct indication of the more specialized condition in the remote descendant. For example, in the series of stages leading to the modern horse, even the earliest known stage, *Eohippus,* already has the digits of the hind foot arranged symmetrically about the middle digit, which is also distinctly enlarged. Merely by a continuous differentiation in the same direction the functionally one-toed foot of the horse has been evolved out of what was already foreshadowed in its remote ancestor.

A different-looking kind of evolution is presented in the comparative series culminating in the strange skull of the pygmy sperm whale. Here the end result is so unlike the earlier stages that we easily recognize a change in the direction of evolution. Such cases may be included under the term "transformation." Nature, however, does not always respect such man-made distinctions and many cases may with respect to one set of features be undeviating or orthogenetic and with regard to other features transformational.

Dollo recognized that irreversibility is not incompatible with great changes in relative sizes or proportions. That

[2] Amer. Nat., 69: 385–403, 1935.

the short may become long and later broad is clearly implied in his interpretation of the history of the foot in the line leading from the arboreal phalangers, with relatively short feet, to the kangaroos, with narrow long feet, thence to the tree-kangaroos, with secondarily widened feet. I also have seen and studied many cases of this sort. For example, the skulls of all known Lower Eocene perissodactyls belonging to the various families ancestral to the horses, tapirs, rhinoceroses, amynodonts, titanotheres, etc., were distinctly long and narrow. In certain lines, such as the long-nosed genera of the titanotheres as studied by Professor Osborn and myself, the skulls became still longer and narrower; in others the long narrow skull of *Eotitanops* gave rise to the broad skulls of *Palaeosyops* and eventually to the still broader skulls of *Brontops, Megacerops* and other highly specialized genera. Similarly, the narrow feet of the earlier perissodactyls, which were relatively small and light-limbed animals, gradually changed into the wide short feet of the later amynodonts, rhinoceroses and titanotheres.

Studies in the evolution of the mammalian molar and premolar teeth[3] have afforded abundant evidence for marked changes in the direction of evolution resulting in diverse transformations in general contour. For example, anteroposteriorly elongate upper cheek teeth, as in many ruminants, extinct South American ungulates, various perissodactyls, certain hystricomorph rodents, glyptodonts and others, appear always to have been derived eventually from molar crowns that were anteroposteriorly short and more or less triangular. In certain lines the primitive triangle was transformed into an elongate parallelogram, as in the wart hogs and elephants; but if we needlessly deprive ourselves of the collateral evidences afforded by earlier fossil mammals of other families, the immediate ancestors of the wart hogs

[3] William K. Gregory, *Proc. Amer. Philos. Soc.*, 73: 169–317, 1934.

and of the elephants reveal only the later and seemingly undeviating stages of the process.

A most striking case of marked shift and even reversal in the direction of evolution is that afforded by the history of the face in the line leading to the baboons. In primitive mammals, such as the opossum and the oldest creodonts, the muzzle was extended in front of the orbits and the axis of the face was but little inclined to that of the basic cranii. Among the Primates this primitive condition is nearly retained in the Eocene family Notharctidae, but in the typical Old World monkeys the face has been much shortened and bent down upon the cranium, as in the macaques. Among the baboons and their relatives one can trace many structural stages in the secondary lengthening of the preorbital face, culminating in the almost dog-like muzzle of the chacma and the mandrill. But this secondary lengthening of the face does not constitute an exception to irreversibility as conceived by Dollo, who recognized marked changes in proportion and held merely that an organ once lost is never regained.

IV. Irreversibility, Polyisomerism and Reversion

Dollo and Abel have dealt with the concept of irreversibility in its application to the study of the evolution of organs and organ systems, but an almost unexplored field is opened if we apply it to the evolution of the morphologic elements of which organs and organ systems are composed. I have elsewhere shown[4] that any given morphological pattern is composed first of polyisomeres or serial elements of similar derivation, and second, of anisomeres, which arise either by the coalescence of polyisomeres or through the differential emphasis of certain polyisomeres or parts of polyisomeres. Polyanisomeres combine the features of both categories. In short, polyisomeres result from budding, fissure or reduplication, an-

[4] *Quart. Rev. Biol.*, 10: 272–290, 1935.

isomeres result from differential increase of particular isomeres without budding.

The vertebral column of the earliest known amphibians was composed of nearly equal polyisomeres with comparatively little regional differentiation, or anisomerism. In most later vertebrates the vertebral column became sharply anisomerous, but in many lines, as among teleost fishes, ichthyosaurs, plesiosaurs, snakes, etc., as well as in cetaceans, a quite secondary de-differentiation or secondary polyisomerism supervened. Primary polyisomeres often grade into secondary polyisomeres and the two are indeed successive phases of the same irreversible evolution.

The power of building or reduplication is especially evident in the history of the cheek teeth in the fossil and recent Cetacea. *Protocetus,* the most primitive of the Eocene archeocetes, possessed the same numbers and kinds of teeth as such primitive placental mammals as the earlier creodonts: namely, three incisors, one canine, four premolars, in each half of both the upper and lower jaws, or forty-four teeth in all. In the squalodonts, according to Kellogg (1928), the total number of teeth rise from fifty-six to "something like one hundred and twenty." There is a large number of teeth in typical members of the Platanistidae, Delphinidae, etc., but in still more specialized forms, such as the xiphioid cetaceans, the number may fall secondarily to one or two pairs or to none at all. Authorities on the Cetacea agree that the high numbers are due to some form of reduplication and the low numbers to secondary reduction. In other words, the Cetacea as a whole illustrate both secondary polyisomerism and secondary anisomerism.

Among the Sirenians the increased number of upper molars is no doubt secondary. Huxley regarded *Otocyon* as an especially primitive genus of Canidae on account of its having four molars, but after studying the dentition as a whole I consider it far more probable that the extra

molar is a new bud from the posterior end of the dental lamina. There are other reasons also for inferring that *Otocyon* is neither a persistently primitive form retaining the fourth molar of a long vanished preplacental ancestor, nor a true reversion to any past stage.

In the light of these concepts, the phenomena that are ordinarily called reversions are seen not to constitute exceptions to the law of irreversibility.

In the case of extra digits on the feet of so-called three-toed horses of the present age, Gegenbaur (1880), from a careful study of several such cases, pointed out that they do not have the same connections with the carpal bones as do the side toes in the feet of the extinct *Hipparion*. Assuredly the extra digits in cats and pigs are merely secondary polyisomeres, not inherited from primitive mammals. A big toe (digit I of the hind foot) is absent in wild Canidae, but a digit in this position often occurs in various stages of reduction in the mastiff and the St. Bernard dog. It is sometimes double, like the extra digits in polydactyl cats. Stockard (1931), after various breedings between St. Bernards with the big toe and Great Danes without it, concludes that the factor for big toe is distinct from the factor for doubling. However this may be, it would be difficult to prove that this so-called big toe is truly homologous with the true first digit of primitive mammals; and the same objection applies to the so-called little toe, which Stockard bred in certain strains of guinea pigs.

"Secondary polyisomerism" is a wide-spread phenomenon which, so far as I know, has been but little noticed by earlier authors. When new polyisomeres are added, as in the case of new cusps in the premolars or new cuspules in the molars, the whole tooth row often tends to be glossed over, so to speak, with the same surface features, so that all the cheek teeth, as in the horses, come to look amazingly like each other. Such newer polyisomeres have a strongly specific stamp and are highly diag-

nostic in value but are often of no greater age than the species or the genus itself. Yet they tend to disguise the older, well-differentiated features which they cover, and thereby they impart a very deceptive appearance of primitive polyisomerism or lack of differentiation. A hasty application of the principle of irreversibility then results in the raising of the new species to generic rank on the ground that it has retained "primitive" features which other species have lost. The same sort of reasoning magnifies the values of the characters used to define supergeneric groups.

In short, uncritical extension of the doctrine of irreversibility to neomorphs, including anisomeres and secondary polyisomeres, has, I believe, contributed to an almost disastrous inflation of our systems of classification, at least in vertebrate paleontology and zoology; genera have thus been inflated into alleged subfamilies, subfamilies into families, families into superfamilies and suborders, and so on; the result being that the classification now very successfully conceals or distorts those broader relationships which the science of taxonomy formerly aimed to express. Some future historian may note that toward the end of the first third of the twentieth century the very abundance of the new discoveries of fossil mammals resulted in obscuring temporarily the grand fact of transformation, which had been so brilliantly expounded by Dollo as the inevitable result of the irreversibility of evolution.

FURTHER NOTES ON PANGENESIS AND THE INHERITANCE OF ACQUIRED CHARACTERS

PROFESSOR CONWAY ZIRKLE
DEPARTMENT OF BOTANY AND MORRIS ARBORETUM,
UNIVERSITY OF PENNSYLVANIA

IN a recent issue of the AMERICAN NATURALIST (September–October, 1935), the writer reprinted a number of ancient and medieval accounts of pangenesis and the inheritance of acquired characters. Indeed, the classical and medieval naturalists, almost without exception, believed that acquired characters were heritable, and from 400 B.C. until the nineteenth century the doctrine was accepted as a matter of course. The hypothesis of pangenesis can also be traced to the fourth century before Christ and, although it was not accepted unanimously, it was believed by the majority of the medieval philosophers and physicians. It is interesting, thus, for us to note that both the doctrine of inheritance that we call Lamarckian and the pangenesis speculations of Darwin were but restatements of accepted classical views.

In the following pages the writer has collected from the older literature a number of passages, not included in the earlier paper, which describe pangenesis and the inheritance of acquired characters. While these excerpts are not very important individually, their number and distribution through the centuries are such that they enable us to view more accurately the historical background of the nineteenth century naturalists. Of course no definitive collection of these passages can be made at present, nor perhaps would such a collection be desirable if enough records could be assembled to show how completely these hypotheses were incorporated in medieval philosophy.

Hippocrates was probably the first to describe pangenesis. He stated, "For the seed comes from all parts

of the body, healthy seed from healthy parts, diseased seed from diseased parts," and he used this concept to explain how somatic modifications could be inherited. Democritos held practically the same views, but Aristotle attacked the doctrine and as a result the classical authorities were divided into two distinct schools. The Galenic literature supported Hippocrates, as did some of the early Christian fathers, although others were undecided. It may be noted parenthetically that patristic literature dealt with the nature and origin of semen in some detail because of certain theological problems concerning the inheritance of original sin and the traduction of the soul of the child from the souls of its parents.

St. Augustine (345–430 A.D.) almost certainly believed in pangenesis, for he described the transfusion (not transmission) of the flesh of the father into that of the son by way of the semen;[1] and two hundred years later, St. Isidore of Seville (622–633 A.D.) stated that semen came from a mixture of the food and the body, a statement which reminds us of Buffon.

During the thirteenth century several philosophers and theologians discussed the mechanism of heredity and the origin of semen. Roger Bacon (1268) explained the progressive shortening of human life by assuming the inheritance of acquired characters, while Bartholomew the Englishman (1240), St. Albert the Great (1254–1256) and St. Thomas Aquinas (1256) indorsed pangenesis. St. Thomas's contribution was a 4,000-word article in his commentary on the sentences of Peter the Lombard. In his "Summa Theologica" (II; Quaest. 81; Art. 1) he described the inheritance of acquired characters as follows:

[1] From "De Genese ad litterarum," Bk. 10, Ch. 1: "Orderliness now seems to demand that we discourse regarding the sin of the first man; but since the Scripture relates about the flesh of the first woman, how it was made, but is silent regarding her soul—it has made us much more intent on inquiring rather diligently as to how those men can or cannot be deceived who believe that just as the flesh is from the flesh, the soul is made from the soul of man by means of the transfusion of the seeds (seminibus) of both these things from the parents into the children."

. . . thus a leper may beget a leper, or a gouty man may be the father of a gouty son, on account of some seminal corruption, although this corruption is not leprosy or gout. . . .

But all these explanations are insufficient. Because, granted that some bodily defects are transmitted by way of origin from parent to child, and granted that even some defects of the soul are transmitted in consequence, on account of a defect in the bodily habit, as in the case of idiots begetting idiots; nevertheless the fact of having a defect, by way of origin seems to exclude the notion of guilt, which is essentially something voluntary.

A late thirteenth century Provençal MS. (D. II, 11; in the Basle University Library) contains two drawings, one of the male, the other of the female generative system, which show the vascular ducts through which the semen was supposedly collected from all the parts of the body. Sudhof, who discovered this MS., printed these illustrations in his "Geschichte der Anatomie im Mittelalter" (Leipsig, 1909), and they were copied by Choulant in his "History and Bibliography of Anatomic Illustration" (Chicago, 1920). They illustrate a conception of "the seminal veins" as old as Hippocrates.

Needham (1934) has recently called the attention of the biologists to a passage in Dante's "Purgatoria" (1318 A.D.), which derives the semen from the excess blood which had acquired its "formative virtue" in the heart. There are many points of interest in this passage (Canto XXV), and it is possible that Dante really believed in a form of pangenesis, although on the surface his derivation of semen from the perfect blood of the heart seems to be inconsistent with even a most liberal interpretation of pangenesis. Three hundred years later, however, Sir Kenelm Digby (1645) stated that the circulatory blood, by coming into contact with all parts of the body, brought back to the heart all the "specific virtues" of the several parts, which were thus made available for the semen. Dante, himself, did not tell how the heart received its "informing" power from all the parts of the body and we can not tell definitely what his ideas were on the subject.

Pierre Bercheur (Petrus Bechorius d. 1362), the noted

theologian, traced the semen no further than to the loins in his well-known work, "Reductorum Moralis" (Bk. 10; ch. 1), but in his account of the famous eel-viper hybridization[2] (Bk. 9; ch. 70) he described the inheritance of a specific somatic modification. Thus:

> According to Iorath and Ambrosius the eel never conceives from its own kind, but from a serpent, which it arouses and leads on by a hissing. Even though the serpent is poisonous in itself, nevertheless, *it belches forth its poison before a union of this kind, so that the eel conceives a non-poisonous offspring,*[3] *in nowise similar to the serpent but like unto itself.* But when the union has been completed the serpent returns to his poison again. The eel is the Blessed Virgin who does not conceive from her own kind, that is to say from man, but rather from God himself and the Holy Ghost, who then because of his venom of justice and severity could be called the serpent; but, to be sure, in this blessed union the serpent (*i.e.* God) has put aside his venom (*i.e.* all justice and severity) and so the eel (*i.e.* the Blessed Virgin) in nowise conceived a venomous or wicked offspring but rather a very kind and gentle one. Moreover, this serpent (*i.e.* God the Father) will on the day of Judgement take up the venom of his severity again, when he shall hand over the sinners to the eternal fires, so that He who, in overlooking men's vices, now seems to lack the venom of severity, shall at that time appear poisonous to them when he punishes their vices.

The fifteenth century physicians followed Hippocrates and Galen rather than Aristotle and consequently the medical incunabula contain a number of descriptions of pangenesis. Two examples are cited. The first is in the work of Antonius Zeno (Policola) who published "De natura humana," Venetiis, 1491, in which he discussed the nature and origin of semen in detail (pp. 30–36). He described pangenesis as follows:

> There are four factors of the sperm:—the matter-factor, the form-factor, the production-factor, and the end-factor. The matter-factor is the fluid of

[2] There are many descriptions of this cross. The story probably arose through a misreading of a passage in Aristotle (*Hist.* An. 5: 540b). The writer has recently reprinted the accounts written by Pliny, Oppian, Athenaos, Aelian, Horapollo Nilous, St. Basil, Achilles Tatios, Philes and Alciati (Zirkle, 1935b). There are many other records, Michael Glycas (c. 1118), Konrad of Megenberg (1350), Raphael Maffejus (1506), "Ortus Sanitatis" (1517), etc.

[3] This is in sharp contrast to the statement of Athenaos ("Deipnos." Bk. 8, ch. 12) who, quoting Andreas, wrote, "Only those lampreys have a fatal bite which come from a viper."

blood which is brought down through the veins to the testes from the whole body and from every member in the manner of an exudation, especially from the principle members (particularly from the brain—according to Hippocrates), and though it is not entirely transformed, yet it is suitable to being transformed.

The second example is furnished by Johannes Peyligk (Peylick) who published "Philosophiae naturalis compendium," Leipsig, 1499. Peyligk denied the possibility of preformationism and described pangenesis as follows (p. 29):

The material portion is the matter of the semen which has flowed down from all the members of the parent himself, from whom are produced the spermatic members. The formative portion is the productive spirit which is formed from three principle spirits; namely, the vital, the natural and the animal: and from other special spirits which are separated in the individual members. And this receives its final form in the testes as the sperm.

Louis Bonaccioli, a French physician, who flourished in the beginning of the sixteenth century, wrote "Enneas muliebris," which probably was first published in 1502. In the passage to be quoted, he does not state that the semen comes from *all* the parts of the body, but he enumerates so many that there is little doubt that he at least believed in a modified pangenesis. From chapter 3:

Obviously (inasmuch as it [the semen] would have to do with food) it starts out chiefly from that part which is the source of food (such as the liver), and especially from its vena cava (which, to be sure obtains a far greater supply of this matter); if for any reason it [the matter] should be lacking in this [part], it is drawn from the other parts which lead from it and tardiness of emission is an indication [of this]. From the heart [the matter comes] through the arteries; from the liver, through the veins; from the brain (although more copiously) through the veins and arteries; but above all from the region of the eyes, which is the most seminal of all the places of the head; you may learn this fact when through venereal union they (the eyes) are changed in exact measure and when through immoderate use of the sexual member the eyes evidently grow weak and feeble, when the strength, of the other parts are not yet failing. From all these [parts], I say, it is at length carried down to the seminal passages and to the testicles in which it receives that divine power of generation. For the vital spirit of begetting, coming down from the heart, becomes fructifying by virtue of the testes, from which it slips down in men to the tube of the penis, in women to the folds of the vulva which have been explained above.

Raphael Maffejus (Volaterranus) published his "Commentiorum urbanorum" in 1506. He described pangenesis in book twenty-four. From p. 746 (Ed. of 1552):

> Semen, which the Greeks call "gouem" as the author Aristotle says, is sent forth among men in a more copious proportion than among the other animals. Hence after coitus a weakness sets in. Moreover, it [the semen] comes forth from the whole body. The similarity of children who resemble their parents in even small markings of the body is proof. In woman, to be sure, as it pleases certain men to state, no semen is given forth, but in its place there is a monthly flow of blood; or if semen is given forth, it is scant (parvum) and is not necessary for conception.

Both Rhodiginus (1516) and Paracelsus (c. 1526) endorsed pangenesis. Jacques Du Bois (Jacobus Sylvius, 1478–1555) also described it in his "De hominis generatione, sive foecunditatis et sterilitatis causis" (1530) as follows:

> Moreover, these differences of semen in quality and quantity, depend upon the organization (or other conditions) of either the whole body or of the chief parts, especially the testes. Having first treated of this [the semen] and of the menstrual blood, we have abundantly demonstrated that the semen is derived from the individual parts, especially from the principle ones. Indeed inasmuch as the testes strain the semen and provide it with its final form, they also must needs affect it according to their own organization.

Nicolas de LaRoche published "De morbis mulierum curandis" in 1542. He describes pangenesis in the female. The female testes are of course ovaries. From chapter 1, section headed "Testes foeminarum":

> For the vasa spermatica attract the matter of the female semen from all parts of the female body and then the testes receive [it] and after it has been received and prepared (cooked), they transmit it to the *parastatae* which are vessels embracing the womb (matrix) which as they recede from the testicles, start to become a little wider until they enter the womb (matrix).

Thomas Vicary, chief surgeon of St. Bartholomew's Hospital, was surgeon to Henry VIII, Edward VI, Queen Mary and Queen Elizabeth. He published "The Anatomie of the Bodie of Man" in 1548. Pangenesis is described in the ninth chapter entitled "The Anatomie of the Hanches and their Parts."

: the which seede of generation commeth from al partes of the body, both of the man and woman, with consent and wyl of al members, and is shed into the place of conceyving, where, through the vertue of Nature it is gathered together in the selles of the matrix of the mother, in whom—by the way of the working of the mans seede, and by the way of suffering of womans seede mixte together, so that eche of them worketh in other, and suffereth in other—there is ingendered Embreon.

Jerome Cardan described pangenesis in 1550, and four years later Jakob Rueff (Ruffus) discussed the origin of semen in some detail. He concluded that it was produced in all the bodily parts and that acquired characters were inherited. From "De conceptu & generatione Hominis," Tiguri, 1554, Chapter 1:

Wherefore it remains to be recognized in the matter of the begetting of humans as in the case of the origin of plants, that since we observe bodies different in respect to their members being produced from one [and the same] semen, we also believe that it [the semen] arises from different parts of the body. Whence have they seen that which they expound?—they who claim that the genital semen is produced only from the brain; since this is less in agreement both with the ratio of mixtures [concoctionum rationi—lit. ratio, reason, manner of digestions] and with the constitution of the body. Indeed, it is certain, that some (and not a small portion) of it is derived from the brain, but the chief portion is gathered from the most important parts of the whole body. For, if we should say that the semen is produced in only one or another part [of the body], anyone will see that this follows by correct reasoning—[namely] that only those same parts should be reproduced. And so, we can rightly say, that in addition to what originates in the brain the semen is produced from the whole body and from all the most important parts thereof; indeed, its effect instructs us as to its cause (origin), especially since in the offspring we see the distinct members perfectly completed to the exact form of the body. Also, against the opinions of others, we have on our side Hippocrates himself, easily the greatest of all physicians; who himself asserted that the seed was gathered from the whole body, and so I say that what is begotten corresponds to the constitution of the begetter—a weak man being born from weak semen and a strong man from strong seed. In addition to these arguments comes the fact that we often observe in children those diseases or defective marks of the body which are present in their parents—things which we entirely believe to have passed into them [the children] through a defect of the seed (genitura). And so, having certainly established these facts regarding the origin and material constitution of the genital semen, these things suffice as a preface.

Pierre Belon used pangenesis to explain the generation of birds in his "L'Historie de la natur des oyseaux." Paris, 1555.

Just as seeds produce such plants as those from which they have been gathered, so animals starting their growth from the seed of their sex, become at length like to those from which they have originated. The seeds are excrements of the bodies, which have the potentialities of those substances from which they have come, and which proceed from the last digestion of the body's food. . . . But the seed of the female being an excrement also, has as a property all the parts of the body, which are engendered from it—not in present action but merely in matter and potienally does it have those parts whereby nature has made the female to be different from the male and hence it happens that sometimes deformed animals engender deformed offspring—at one time, male and another time female.

Levinus Lemnius, a Dutch physician, explained the inheritance of disease by pangenesis, and Ambrose Paré (Ambrosius Paraeus, 1517–1590), although his identification of fertile and sterile semen were directly opposed to those of Lemnius, described pangenesis and the inheritance of disease just as Lemnius did. From the preface to his "De hominis generatione" (1573):

. . . Good semen ought to be white, shiny, sticky, globular with the odor of the elder or the palm-tree, liked by bees, and in water it sinks to the bottom (literally—sinkable to the bottom of water); for that which floats, is considered unfruitful.[4] Indeed, a great portion of it (comes) from the brain, but as a whole it is derived from the entire body and from its individual particles, both solid and soft. For, unless in its entirety, it flowed down from the whole body, all the individual parts of the foetus would hardly be formed therefrom; since, indeed, like things are made from like. From this it follows that the foetus resembles its parents not only in form and appearance; but also in the formation of the limbs and in the inter-connection of the internal parts–; to such an extent that diseases become hereditary when a weakness of this or that organ (e.-viscus) is transferred to the offspring.

Yet there are those who think that this derivation of semen from the entire body ought not to be understood [as consisting of] bulk and material since the part of all the blood which is weakened is only a certain portion; but rather as consisting of energy and the formative power; to be sure only the natural and vital animal spirits from the individual parts are the artizans of formation and of life; and these and the formative force flow down into the semen which is produced by the testicles. (They say) that their argument is the fact that several foetuses whole and complete in the number of all their parts are produced from maimed parents.

[4] Many philosophers believed the exact opposite of this. Hippocrates thought that semen was fertile only when it was foamy. Aristotle held that semen was discharged by means of a blast of air, and that the air gave it fertility. Lemnius stated that coition was a churning of air into the semen. Air itself was supposedly sufficient to fertilize the females of a number of species.

Girolamo Mercuriale (1530–1606) published "De morbis muliebribus" in 1582. He quotes and endorses Hippocrates on the origin of semen in the section headed "Signa sterilitatis."

If by a defect of the semen, then, there is no other means of knowing, except by a knowledge of the constitution of the entire body: because it is the opinion of Hippocrates, in the book on air, water and places, likewise in his book on generation and elsewhere that: "The Semen separates from the entire body"; and so, as the body is constituted, so is the semen; thus, by whatever symptoms an abnormality of the body shall be recognized, by those very same symptoms shall abnormality and defect of the sperm be discovered. . . .

Albertini Bottoni held that semen was an excretion, but admitted that it had its uses. In "De morbis muliebribus" (1585) he stated that it was apt to produce structures similar to those in its place of origin. From Ch. 41:

For although the semen is an excretory fluid, it is nevertheless a useful one and in addition it is fruitful by its nature, and copiously filled with the spirit of life and when taken up in a suitable matrix, it is apt to produce (something) similar to that from which it had been derived. The menstrual blood likewise, although it is held to be the excretion of the whole mass of blood nevertheless exerts no influence on the whole body but customarily brings on a vexation in non-pregnant and non-lactating women.

Mauricius Cordae in a somewhat obscure passage in his "Commentarii in librum priorem Hippocratis Coi de mulieribus" (1585) supports pangenesis. From commentary number 6:

When this happens, it is now rightly asked whether the semen ought to be considered as derived from every part or whether it (arises) rather from a perfusion of spirit and heat. Just as the chief parts are all joined to one another by communicating vessels and all the veins, nerves and arteries are continuous down to the testes and even penetrate and permeate them; so there is a meeting of spirits of every kind especially from these sources, together with heat and there is a coming together not without a violent impulse and a spasm as of heat (?), in this manner from the remaining parts, which seize and carry with them an image of some one of them although not without other things.

Archangelo Piccolhomini described pangenesis in "Anatomicae praelectiones explicantes," Rome, 1586. The following quotation was incorporated in a footnote in

Caspar Bauhin's "Theatrum anatomicum," Francofurti, 1635, (p. 567):

The next matter of the semen goes forth from all the parts of the body and especially from the principle viscera: it is nothing else but food which has overflowed from the optimal nutrition of the parts; for nature prefers that there be too much nourishment rather than too little. This [nourishment] is then changed by the parts and when abandoned by assimilation [i. e.—when the process of assimilation has finished working on it] it has received the strength [power] of the parts. Wherefore, the nourishment which overflows from the nutrition and assimilation of the brain is the nearest (proxima) matter from which will be developed that portion of the fecund semen, from which the brain of the foetus itself will be produced. Now, when the nourishment overflowing in the brain cannot reach the testes because of the cutting of those veins, then they [the testes] become unfruitful. In the same manner, men will become sterile if the vein which leads from the heart or from the liver is cut; since it is especially the overflowing nourishment, or seminal material of these parts, which is the cause of the semen becoming fertile.

Seventeenth century records of pangenesis and of the inheritance of acquired characters are doubtless quite numerous and new ones will probably be discovered by any one who examines the medical literature of the time. The writer (1935a) quoted two such records (Venette, 1687, and Ray, 1691) and Needham (1934) has called attention to the fact that both Sir Kenelm Digby (1645) and Nathaniel Highmore (1651) explained inheritance by means of pangenesis.

Sir Kenelm Digby's contribution appeared in his "Immortality of Reasonable Souls." He did not believe that the semen itself came from all parts of the body, and he stated the hypothesis in this form only to refute it. From Ch. 23; p. 265:

To deduce this from its origine, we may remember how our Masters tell us, that when any living creature is passed the heat of its augmentation or growing; the superfluous nourishment settleth itself in some appointed place of the body to serve for the production of some other. Now it is evident that this superfluity cometh from all parts of the body, and may be said to contain in it after some sort the perfection of whole living creature. Be it how it will, it is manifest that the living creature is made of this superfluous moysture of the parent: which, according to the opinion of some, being compounded of severall parts derived from the several limbs of the parent; those parts when they come to be fermented in convenient heat and moisture, do take their posture and situation, according to the posture and disposition

of parts that the living creature had from whence they issued: and then they growing daily greater and solider, (the effects of moysture and of heat;) do at the length become such a creature as that was, from whence they had their origine.

Which an accident that I remember, seemeth much to confirm. It was of a cat that had its tail cut off when it was very young: which cat happening afterwards to have young ones, half the kitlings proved without tails, and the other half had them in an ordinary manner;[5] as if nature could supply but one partner's side, not on both. And another particular that I saw when I was at Algiers, maketh to this purpose, which was of a woman that having two thumbs upon the left hand; foure daughters that she had did all resemble her in the same accident, and so did a little child, a girl of her eldest daughters; but none of her sonnes. Whiles I was there I had a particular curiosity to see them all; and though it be not easily permitted unto Christians to speak familiarly with Mohametan women; yet the conditions I was in there, and the civility of the Bassha, gave me the opportunity of full view and discourse with them: and the old woman told me, that her mother and grandmother had been in the same manner. But for them it resteth upon her credit: the others I saw myself.

The arguments used by Digby to prove that the semen itself did not come from the entire body are not important in themselves. He really accepted pangenesis, however, and he looked upon the blood as the vehicle for the collection and transmission of the specific formative virtue.

But we should be to blame to leave our Reader without clearing that difficulty, which cannot choose but have sprung up in his thoughts, by occasion of the relations we made at the entrance into this point concerning the cat whose kitlings were half with tails, and half without: and the womans daughters at Algiers, that had as well as their mother excrescences upon their left thumbs, imitating another lesser thumb: and the like effects whensoever they happen, which they do frequently enough.

[5] The kittens appeared in the fundamental Mendelian one-to-one ratio. Mendelian segregation had already been described a number of times under the heading "degeneration" (Zirkle, 1935 b), but no previous recording of ratios has yet been found. Six years later Highmore (1651) also described a one-to-one ratio, this time in puppies. These meaningless observations preceded by just over two hundred years the first really authentic record of a Mendelian ratio which has come to light. Whiting (1935) has pointed out that Dzierzon (1854) in the "Bienenfreund aus Schlesien" described a one-to-one ratio in bees, fourteen years before Mendel published. The excerpt from Dzierzon: "One must be completely certain that the queen belongs to the genuine species by birth. If she herself has come from the hybrid-brood (Bastardbrut), then it is impossible for her to produce drones, unless she produces half Italian and half German drones—but what is noteworthy—this is not qualitative but quantitative; as if it were hard for nature to combine the two types into a middle species."

Let him therefore remember, how we have determined that generation is made of the bloud, which being dispersed into all parts of the body to irrigate every one of them; and to convey fitting spirits into them from their source or shop where they are forged; so much of it as is superabundant to the nourishing of these parts is sent back again to the heart to recover the warmth and spirits it hath lost by so long a journey. By which perpetual course of a continued circulation, it is evident that the bloud in running thus through all the parts of the body must needs receive some particular concoction or impression from every one of them. And by consequence, if there be any speciall virtue in one part which is not in another then the bloud returning from thence must be endued with the virtue of that part. And the purest part of this bloud, being extracted like a quintessence out of the whole masse, is reserved in convenient receptacles or vessels till there be use of it: and is the matter or seed, of which a new animall is to be made; in whom, will appear the effect of all the specificall virtues drawn by the blood in its iterated courses, by its circular motion, through all the severall parts of the parents body.

Whence it followeth, that if any part be wanting in the body whereof this seed is made, or be superabundant in it; whose virtue is not in the rest of the body, or whose superabundance is not allaid by the rest of the body; the virtue of that part, cannot be in the bloud, or will be too strong in the bloud, and by consequence, it can not be at all, or it will be too much in the seed. And the effect proceeding from the seed, that is, the young animall will come into the world savouring of that origine; unlesse the mothers seed, do supply or temper what the fathers was defective or superabundant in; or contrariwise the fathers do correct the errours of the mothers. . . .

. . . But to go on with our intended discourse. The seed, thus imbued with the specificall virtues of all the severall parts of the parents body, meeting in a fit receptacle the other parents seed; and being there duly concocted, becometh first a heart: which heart in this tender beginning of a new animal containeth the severall virtues of all the parts that aferwards will grow out of it, and be in the future animal; in the same manner as the heart of a complete animal containeth in it the specifike virtues of all the severall parts of its own body, by reason of the blouds continuall resorting to it in a circle from all parts of its body, and its being nourished by that juice to supply the continual consumption which the extreme heat of it must needs continually occasion in its own substance; whereby the heart becometh in a manner the compendium or abridgement of the whole animal.

Nathaniel Highmore gave his conception of the mechanism of heredity in his "*History of Generation,*" London, 1651. He disagreed with Digby in most details, yet he advocated pangenesis. His conception of the formation of semen was essentially that of Buffon. He held that our food consists of a great variety of elements because every part of the body requires a different type of

element for its repair and reconstruction. Highmore comments upon the views of Digby as follows (from p. 29):

For the material part of this seed, there is a large dispute whether it be *a toto vel a parte decisum*. I shall not stand to tell you the names of those who are Patrons of the one, and of the other; nor rehearse their arguments. If you examine them, you shall finde theirs most rational, that affirm the decision from the whole body; what we finde more particularly discours't of our forementioned author, in his 24th chapter [Kenelm Digby-Discourse of Bodies], we shall take up and a little review. Where he hath truly and fully evicted the wand'ring phancies of some, that would have this compound of severall parts, to be collected from every particle, so as passing by or through every little atome of the Parents body, in its passage; should be impregnated, and imbued with the nature of it, and so retire to the reserve where it is kept for generation. And afterwards these particles being fermented by convenient heat, do take their posture and scituation; according to the posture and dispositions of those atomes they visited in their passage, and from whom they received those imbibed natures. But this circulating our Author tells us, is impossible. I will not wrong him so much as to rank his more solid reasons with my own. Could we finde these chanels and conveighances in the Body, by which this matter should pass; yet I might doubt of the unquestionable verity of this doctrine. For what should hinder this matter circulating about the Body, from receiving qualities, and so likewise the nature of every part it passeth by; and so every particle of this matter, should be impregnated with the natures of the whole; and every small Atome should become a living Creature, or else the Subsequent should blot out the Antecedent Character and the Impression should be only from the last Part. We may likewise as truly, as safely conclude with our Author, that it is impossible for every little part to remit some parts impregnated with the nature of that whole part from which it fell. This by some is thought to be done by that *Quasi Epilepsia in Coitu*, that kinde of convulsion or concussion of the parts, by which is shook off from them somewhat retaining the nature, and property of every part, and these being joyned make up the seed. This seems to be very much befriended by our Authors relation of the cats kitned without tails; and of the Womans daughters with six fingers upon a hand. Myself also have seen a kinde of Poultry without rumps: which breeding with their own kind still brought forth Chicken wanting that part: if with others, sometimes they had rumps, sometimes but part of a rump. And not long since I saw a Mungril Bitch, that had her tail cut close to her body almost, whose Whelps were half without tails, and half with tails: the next year following, she brought them forth all with long tails, as she had before the cutting off. Which though it seems to favor (as I said) this opinion, it; as may appear by the frequent perfect generations of mutilated creatures; which beget children or issue with two legs or arms though they had but one; Spaigniels, whose tails are always cut, bring forth Whelps whose tails need as much cutting, as their Dams or Sires did. Wee must therefore look out some other way, how this may be done without the parts themselves.

Antoine Legrand, the Augustinian missionary to England, published "Institutio philosophica secundum principici D. Renati Descartes" in 1672 and in the next year his "Historia naturae." In both of these works he described how the semen collected from all parts of the body and thus how mutilations could be inherited. From "Institutio philosophica." (Pt. 8; Ch. 4; § 2):

However, in order that it might be understood by what device an Animal can be shaped from such a formless fluid so that it should have any resemblance to the element (principium) from which it was produced, it is necessary to suppose that the Semen of the Male as well as that of the Female flows down from all the parts of their bodies, so that there is no member from which something of the *seed of generation* is not separated. For just as a serous fluid is separated from the whole body through the Veins and is stored through "emulgentes" [probably—drain-ducts] in the Kidneys and the Bladder, where at a given moment an ejection occurs; so why not, since double Veins and a like number of Arteries go to the Testes—why should not the Seminal parts flow into these (Veins and Arteries) from the whole body and then from them into appointed vessels?

And this does not occur gradually and with any preparation of the "materia," but it happens in a rather short space of time, in which the whole body is so aroused to excretion, that whatever there is in the (several) parts that is very life-giving (spirituosum) is moved, squeezed forth and then hastens off.

The inheritance of mutilations is described in the following ("Historia naturae," Pt. 8; Art. 2; Ch. 2):

And it is this Semen which the Animal uses for the procreation of those like unto himself. But if the animal from which the Materia Spermatica is produced, happens to lack any member (or to be overburdened by the superfluity of any part) then the virtue of that member will not be in the blood, and therefore the offspring will be born maimed and lacking some part. If, in truth, parts (of the body) of the animal are multiplied as *Digbaeus* mentions in his *African Women*, or, if a superfluity accreses, it will effect a deformity in the offspring also; unless this superfluity is balanced in the semen of the other parent, or the over-abundance of the blood (*i.e.* the over-abundance in the blood of the virtue of the excrescent part) is corrected.

Legrand showed that the evidence used by certain philosophers to prove that the semen was produced in the brain could be given another interpretation.

Excessive effusion of *Semen* is most dangerous to the Brain and the Nerves and produces a noticeable weakness in these parts; as (may be seen in) those

who indulge too much in *Venery* or befoul themselves with filthy contaminations. Hippocrates once thought, and it is even now believed by many physicans that the genital fluid flows off into vasa spermatica from the *brain*, and that when an emptying of this fluid occurs, the strength of the brain, is necessarily weakened. Indeed, since there are no special ducts from the brain which might bring the afore-said fluid down to the spermatic parts, it is reasonable to admit that this noble fluid is produced from the *Massa Sanguinaria*, some part of which is sent off to the genitalia no less than to the brain itself. As for the fact that excessive loss of genital fluid has a destructive effect upon the brain and brings about a weakness of that (organ), that arises from the fact that the *Blood* restores what is lost through the effusion of the semen that has been released, and supplies the brain with a thinner portion of itself; since the greatest supply of the animal spirits is [then] assigned to the spermatic parts. To be sure, since the Blood from its own substance cannot lavish sufficient upon the Genitals, it absorbs additional matter from the brain and demands back what has previously been assigned [to the brain] in order to recompense here.

Marcello Malpighi, who, together with Nehemiah Grew, founded plant anatomy, described pangenesis in his essay on the kidneys. The passage is in his "Opera Omnia" (London, 1687). From Pt. II, p. 289:

But, it is probable, moreover, that it [the semen] is formed from the retention of these particles, inasmuch as the substance proceeding either from the whole [body] or from the blood is a deflux (decidua) of tiny particles of semen; wherefore the mass of blood, wheresoever driven from the structure of the glands which are in the kidneys, is freed from the "exalted" salts and impurities (filth): the fermentation is kept up more easily, the first beginnings [rudimenta] of similar and dissimilar parts are brought down and separated in the work-shop of the testes and then when the semen is regathered it is more fecund.

Martin Schurig wrote an excellent review of the various theories concerning the origin of semen in his "Spermatologia historico-medica" (Frankfort a. M., 1720). His own views (Ch. 1; Part 11) are not definitely in favor of pangenesis, although he conceded the probability that the particles of semen are derived from the blood stream and are filtered out and collected in the testes.

Accordingly, I believe that in the testicles, that is to say, in these vasculoglandular parts—because of their peculiar conformation, there occurs the secretion or translocation of a peculiar fluid, different from all others (*i.e.* the seminal fluid). On the other hand, I am quite willing to concede that such spermatic particles just like others, *e.g.* the bilious particles, are hiding in the blood and with the same, by means of the circulation (of the blood) are

brought through the arteries to the testicles, and then through the afore-mentioned peculiar vessels are separated into a fluid impregnated with the various qualities of its kind, and finally it is conserved according to the manner recounted by other Authors.

CONCLUSIONS

Belief in the inheritance of acquired characters can be traced back to the time of Hippocrates. From the fourth century before Christ until the nineteenth century it was accepted as a matter of course; indeed, Brock noted but two individuals during this period who definitely did not believe that such characters were heritable, although there were doubtless others. On the other hand, there are many who described the inheritance of such characters. Among the latter are Hippocrates (c. 400 B. C.), Aristotle (384–321 B. C.), Galen (?)(130–220 A. D.), St. Thomas Aquinas (1256), Roger Bacon (1268), Pierre Bercheur (d. 1362), Sylvius (cit. Osborne), Jerome Cardan (1550), Jakob Rueff (1554), Levinus Lemnius (1561), Ambrose Paré (1573), Sir Kenelm Digby (1645), Nathaniel Highmore (1651), Antoine Legrand (1672), John Ray (1691), Michael Adanson (1763), Erasmus Darwin (1794) and Johann Friedrich Blumenbach (1795). Lamarck's contribution to biological theory was to assume that the inheritance of somatic modifications was cumulative from generation to generation so that ultimately new species were formed from the older ones.

Belief in pangenesis can also be traced to the fourth century before Christ. The classical and medieval philosophers, however, were not unanimous in support of the doctrine, probably because of Aristotle's opposition. In many cases it is very difficult for us to determine their attitude toward the hypothesis, for many who traced the semen to some particular organ, such as the cerebrum, liver, heart, kidneys, testes, etc., need not have been opposed to pangenesis. Often those who supported the view that the semen was derived from all parts of the body traced it to these same organs, where, they thought, it was only stored temporarily. Among those who defi-

nitely supported pangenesis are Hippocrates (c. 400 B. C.), Democritos (c. 400 B. C.), Galen (?)(130–200 A. D.), Clement of Alexandria (193–211), St. Isidore of Seville (622–633), Bartholomew, the Englishman (1230–1240), St. Albert the Great (1254–1256), St. Thomas Aquinas (1256), Peter of Crescentius (?)(1305), Antonius Zeno (1491), Johannes Peyligk (1499), Louis Bonaccioli (1502), Raphael Maffejus (1506), Ludovicus Rhodiginus (1516), Paracelsus (c. 1526), Jacques DuBois (1530), Nicolas de La Roche (1542), Thomas Vicary (1548), Jerome Cardan (1550), Jakob Rueff (1554), Pierre Belon (1555), Levinus Lemnius (1561), Ambrose Paré (1573), Girolamo Mercurale (1582), Mauricius Cordae (1585), Albertinus Bottoni (1585), Archangelo Piccolohomini (1586), Sir Kenelm Digby (1645), Nathaniel Highmore (1651), Antoine Legrand (1672), Nicolas Venette (1683), Marcello Malpighi (1687), John Ray (1691), de Buffon (1750), de Maupertius (1756), Albrect von Haller (1781), Charles Bonnet (1781) and Herbert Spencer (1864). These names probably represent but a small fraction of the total.

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THE FOOD OF INSECTS AND ITS RELATION TO RESISTANCE OF PLANTS TO INSECT ATTACK[1, 2]

PROFESSOR REGINALD H. PAINTER
ASSOCIATE PROFESSOR OF ENTOMOLOGY, KANSAS AGRICULTURAL EXPERIMENT STATION

A STUDY of the resistance of crop plants to insect attack has served to emphasize the great importance of food habits in the biology and evolution of plant-feeding insects. The evidence is accumulating that two plants, identical outwardly, may differ widely in nutritive value to an insect species as measured by the insect's ability to maintain a population on them.

Resistance of plants to insect attack may be defined as the relative amount of qualities possessed by the plant which influence the ultimate degree of damage done. For practical purposes it represents the ability of a crop plant to produce a larger crop than do ordinary varieties at the same level of insect population. This difference in yield is a measure of the economic value of resistance, but is, however, dependent on many factors as well as resistance to insects.

It should be the purpose of projects on insect resistance in crop plants to produce varieties not only as good or better in respect to agronomic characters and disease resistance than those now available, but also resistant to one or more insects. Thus the breeding of crop plants resistant to insect attack becomes part of the entomologist's contribution to the crop improvement program of a particular crop and, conversely, insect resistance should

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become one of the objects of study in each crop improvement project.

The place which plant resistance occupies in a program of insect control will vary with each crop and insect. Frequently it will be only a contributing feature. Occasionally it may be the chief means of controlling a pest. Sometimes the study of a case of insect resistance will serve only to prevent the distribution of varieties more susceptible than those now in use. In the case of each common injurious insect and each crop plant the possibilities of the use of resistant varieties need to be examined.

The more apparent causes or factors which enter into resistance and related phenomena in various plants, together with references to a few examples, may be outlined as follows:

FACTORS IN THE RESISTANCE OF PLANTS TO INSECT ATTACK

I. Evasion: Transitory or pseudo-resistance by avoidance.
  A. Time of maturity. (Genetic and ecological.)
    (Boll weevil and cotton; Isley; 1934.)
  B. Soil conditions. (Largely ecological.)
    (*Phylloxera* and grape; Nougaret and Lepham; 1928.)
    (*Aphis rumicis* and *Vicia faba;* Davidson; 1925.)
  C. Water balance. (Largely ecological.)
    (Cotton stainer; Mumford; 1926.)

II. Resistance and tolerance: (Largely genetic.)
  A. Resistance mechanisms largely of plant origin.
    (1) Resistance to diseases carried by insects.
      (*Eutettix tennellus* and curly top of sugar beet; Carsner; 1933.)
    (2) Passive resistance; resistance due to mechanical barriers, such as hairs, cuticle, etc.
      (Leaf-hoppers and soy-beans; Johnson and Hollowell; 1935.)
    (3) Active resistance.
      (a) Repair and recovery.
        (Corn-root worm and corn; Bigger; 1935.)
      (b) Tolerance mechanisms.
        (Corn or sorghum and chinch bugs (in part); Painter *et al.*, 1935; Snelling *et al.*, 1936.)
      (c) Destruction of eggs and other stages by cell proliferation.
        (Boll weevil and cotton; Hinds; 1906.)
      (d) Habit of growth.
        (Onion thrips; Jones *et al.*, 1935.)
  B. Resistance mechanisms requiring an insect counterpart.[3]

[3] Examples discussed below.

(Largely genetic in both plants and insects.)
(1) Oviposition responses.
(a) To surfaces.
(b) To odorous substances.
(c) To habit of growth of plant.
(2) Mechanisms related to feeding with the following results for the insects:
(a) Abnormal length of life.
(b) High mortality.
(c) Reduced size.
(d) Reduced fecundity.
III. Immunity. (Largely genetic.)

An immune variety, if defined as a variety which a specific insect will never consume or injure under any condition, does not exist as far as present knowledge goes. In particular, among some cases of the resistance to aphids cited later in this paper there are examples of resistance that approach immunity. In the case of the relationship of most insects to plants it is to be expected that resistance will be relative and must be measured in terms of the susceptible or commonly grown varieties. Hence plant resistance may commonly be expected to vary with the intensity of the insect infestation. Injury of an ordinarily resistant variety, when in the presence of a heavy infestation, does not constitute proof of susceptibility unless the injury to susceptible varieties and to the ordinarily resistant variety is equal in all respects. A variety which carries only a relatively low order of resistance may be of considerable economic importance even if badly injured by occasional heavy infestation.

There are at least four reasons for the study of the cause of resistance. The most important is to differentiate cases of evasion or escape from those in which the resistance factor is stable under a wide range of conditions. Such a factor, when genetic, may be incorporated into desirable varieties. When evasion is due to earliness resulting from genetic characters it may also be of use in insect control. The importance of evasion is shown by the increased use of quick-maturing cotton varieties during the earlier days of the Mexican cotton boll weevil invasion. The manipulation of ecological

factors is a valuable adjunct in insect control. Yet ecological changes must be made repeatedly and when concerned with crops are subject to the exigencies of farm practice and fluctuations of the weather. With the exception of records concerning "date of planting" there is relatively little actual data indicating the possibility of resistance induced by ecological means. On the other hand, there are numerous cases in which resistance to insect attack is inherited and may be incorporated into desirable plant varieties. In this connection, however, it must be remembered that the thing inherited is not resistance as such, but the ability to react repeatedly with the same environment, both biological and physical, in a certain way. Some of the hybrids from a cross between resistant and susceptible plant varieties may be expected to react like the parents when under the same conditions. Others may be intermediate or may occasionally surpass either parent in resistance or susceptibility. If the environment, either physical or biological, or both, is changed the reaction of both parents and hybrids may be changed. Thus wheat varieties and hybrids that react as resistant to the Hessian fly in the hard wheat belt of Kansas or in California are susceptible in the soft wheat belt of eastern Kansas and in some states further east. This does not invalidate conclusions regarding resistance, previously reached.

A second reason for the study of cases of resistance is to enable the plant breeder to differentiate the several genetic factors that may be involved and their method of operation. Some cases of resistance have been shown to be due to single genetic factors, while others appear to be associated with multiple factors. Different resistant varieties may carry different genetic factors which give the same degree of resistance but attain it through different means. On the other hand, the same variety may carry two or more genetic factors for resistance. Thus Marquillo wheat usually carries a lower egg count and also lower larvae survival of Hessian fly than most other wheat varieties. Some evidence at hand indicates that

these two factors in the resistance of Marquillo are the result of different genes. It is especially important to know whether the different genetic factors are cumulative in their effect on the level of resistance.

A study of the cause of resistance is of importance in its relation to a knowledge of the biology of the insect studied. The tropisms and other reactions of an insect sometimes stand out in sharper contrast against the background of different varieties. Thus the study of varieties has added to the knowledge of the relationship of the European corn borer to tall, vigorous growing corn. (Neiswander and Huber, 1929.)

The study of the cause of resistance has frequently been emphasized because a visible factor is of value in the selection of resistant plants. The danger in this use is emphasized below. In addition, if selections made in this manner are not continually tested against the insect, there is a possibility of loss of modifying factors that may be of importance.

It is necessary to be cautious in assigning an inherited factor as the "cause" in a case of resistance to insect attack. Genetically such a factor may be:

(1) The actual *modus operandi* of resistance.
(2) One of the multiple effects of a gene operating to cause resistance in some other way. That is to say, the actual cause of resistance may be one effect of a gene which is also visible in some character inherited parallel with resistance.
(3) A gene which is closely linked with the one causing resistance.
(4) One of a group of genes giving the same phenotypic reaction but not all connected with resistance.

It should also be remembered that resistance and its cause may themselves result from multiple factors, only one of which may be associated with the cause assigned. In spite of the genetic complications it has been possible to make progress in breeding plants resistant to insect attack without knowing in detail the cause of such resistance.

Resistance may and frequently does result from a combination of two or more of these factors. Some factors or causes of resistance, notably those which may be

grouped under I and IIA, have been summarized in various places.

Those mechanisms of resistance which require an insect counterpart have not been emphasized sufficiently in summaries of studies in insect resistance. They concern some character of the plant which calls forth a physiological or tropistic reaction on the part of the insect to complete the quality of resistance or susceptibility. They concern mostly the food relationships of the insect and are of the nature of interdependent reactions between plant and insect. Through the last hundred years of entomological and botanical literature, examples are widely scattered, but when brought together shed some light on the problems involved. It is the purpose of this paper to bring together a number of these examples, especially the more recent ones, show their bearing on various entomological problems and suggest possible physiological explanations.

The food relationships between insects and plants are especially apparent at three points in insect life history: (1) At time of oviposition by the female or location of food plant by the young larvae; (2) at time of commencement of feeding by the young larvae or nymphs; (3) in the effect of nutrition on the later stages, especially on mortality in the last instar before reaching the adult stage, in length of adult stage and in fecundity of the female.

The attractiveness of a plant for oviposition or when sought as a food plant for an insect frequently appears to involve the character of the surface or chemical compounds which give off odors. These characters belong in the group of factors under consideration only to the extent that the attractiveness or lack of it involves tropisms on the part of the insect. The character of the surfaces available for oviposition have been mentioned as one of the causes of resistance. The hairiness or thickness of the epidermis usually represents only passive mechanical resistance, though negative responses in the ovipositing insects may be involved. The hairiness of various

legumes and cotton have sometimes been assigned as one cause of the resistance of certain varieties to leaf-hoppers (Hollowell *et al.,* 1927; Pieters, 1928; Parnell, 1925; Johnson and Hollowell, 1935). Jewett (1932) has shown, however, that some other factors besides pubescence are involved in the case of alfalfa and clover. One of these may be the ease with which the leaf epidermis of the several varieties may be punctured. (Jewett, 1933, 1935.) He relates this factor to the feeding of the insects, but if the difference occurs on the stems it may also be related to oviposition. Poos and Smith (1931) also have shown that factors other than pubescence are of more importance in differences in the oviposition of the potato leafhopper *Empoasca fabae* on varieties of its food plants.

The toughness of the epidermis and associated cells has been cited as one factor in resistance to insect attack, especially among insects ovipositing or feeding in fruits. (Boyce, 1933.)

A few cases of differential oviposition on host varieties have been recorded without assigning a cause for the differences in tropistic reaction. Holloway (1935) has recorded differences in the size of egg clusters of the sugar cane borer (*Diatraea saccharalis*) on various varieties of sugar cane.

McColloch (1918) has shown that each of four varieties of durum wheats had fewer Hessian fly eggs laid on them than did Marquis spring or the winter wheats studied. Packard (by letter) has called the writer's attention to the fact that Marquillo, a hybrid between Marquis, *vulgare,* and Iumillo, *durum,* wheat shows the same lower oviposition rate. In a count of a light infestation in the field in 1935 there were 8 times as many eggs laid on Ceres as on Marquillo wheat planted in an adjacent row. Counts of eggs were made on six replications. This low attractiveness to Hessian fly females appears to have been transferred in some cases to winter segregates of crosses between Marquillo and winter wheats. Thus a character resulting in a low rate of oviposition appears to have been transferred from a durum wheat

(*Triticum durum*) to a common spring wheat (*T. vulgare*) and then to a winter type (*T. vulgare*). The character of the wheat plant which brings about this low oviposition rate is unknown. It and the other cases cited may be related to the character of the leaf surface or to odor. In either case it is not surprising to find it inherited.

The habit and vigor of growth is a feature of plant development that has an influence on insect reproduction. Both are greatly influenced by local soil and edaphic conditions in addition to variety characteristics and adaptation. It has been suggested, for instance, that the relative erectness of leaf blades in wheat was the reason for differences in the number of eggs laid on different leaves of the same plant or of different plants. Position is, however, only one of several possible reasons. Hybrid vigor has been shown to be a factor in the resistance of corn and sorghum hybrids to chinch bugs. Whether there is any effect on oviposition is yet unknown. The European corn borer selects tall vigorous corn for oviposition (Neiswander and Huber, 1929). These characteristics may be due to variety or to ecological conditions or both. The relative difference in acceptability for oviposition of two varieties planted under different conditions of soil or date of planting, remains the same, though the more resistant variety of one experimental plot may carry a larger number of eggs than the susceptible variety in another plot. Such occurrences serve to emphasize the fact that, so far as is known, resistance is relative and varieties must be compared, as far as possible, at equivalent stages of development.

MECHANISMS OF RESISTANCE RELATED TO FEEDING

The usual classification of phytophagous insects into the groups polyphagous, oligophagous and monophagous is useful but essentially misleading, since it disguises the actual conditions and is only a classification of the apparent foods. It necessarily is based on lists of plants which insects eat rather than those which furnish equal

nutriment. It can be demonstrated that varieties of a single host species or even parts of individual plants may differ in respect to nutriment. On the other hand, biological races of a single insect species may belong under different categories. Thus the European corn-borer strain with a single brood is practically monophagous, while the multiple brooded strain is polyphagous. Only if such modifications are kept in mind is the classification useful. Related to this problem is the tendency to interpret food relations of insects on the basis of relative acceptability as human food. Statements are frequent in the literature that a given insect did not feed on a certain plant because it was not as succulent as or more fibrous than its normal food. Less anthropomorphic explanations are probably nearer the truth.

Insects Developing on a Wider Range of Hosts

Many entomologists would consider the gipsy-moth, grasshoppers, cutworms and the corn-ear worm as belonging among the so-called polyphagous species. In a study of 149 food plants of the gipsy-moth, Mosher (1915) found 42 species of plants that were "favored food," 13 species that were "favored food" after the early larval stages, 32 species on which a small proportion of gipsy-moth larvae developed and 62 species that were unfavored food. Evidently this fairly omnivorous Lepidopteron could not assimulate equally well all kinds of vegetable matter which it will eat.

Hodge (1933) in rearing in separate containers individuals of *Melanoplus differentialis* from egg to adult on single food plants, found a range of mortality from 28 per cent. on wheat to 95.7 per cent. on oats. (Table I.) There was a mortality of 78.6 per cent. on lettuce, but all adults reared on both oats and lettuce died within 48 hours. The tropistic reactions, growth curves and susceptibility to disease in the case of insects reared on the two latter plants are suggestive of a condition analogous to vitamin deficiency.

In a study of the development of the pale western cut-

TABLE I

MORTALITY OF MELANOPLUS DIFFERENTIALIS REARED ON VARIOUS FOOD PLANTS. (FROM HODGE, 1933.)

Diet	Original No.	No. transformed	Per cent. transformed	Per cent. died	
Mixed	14	10	82.6	17.4	Adults vigorous normal fertile
Wheat	25	18	72.0	28.0	
Barley	18	8	44.4	55.6	
Rye	19	8	42.1	57.9	
Lettuce ...	28	6	21.4	78.6	Adults ± dead within 48 hours
Oats	23	1	4.3	95.7	Adults died on day of emergence

worm on various food plants, Seamans and McMillon (1935) found a range of from 5.5 per cent. to 85 per cent. in mortality. The mortality was slightly higher (85 per cent.) on wandering Jew (*Tradescantia* sp.) than on wet wheat stubble (84 per cent.).

In the case of the cotton boll worm (*Heliothis obsoleta*), Isley (1935) has found that it took twice as long for larval development on tomato stems and foliage as on corn ears. Various other host plants were intermediate (Table II). The degree of mortality paralleled the

TABLE II

THE DURATION OF LARVAL STAGE AND FECUNDITY OF HELIOTHIS OBSOLETA REARED ON VARIOUS HOST PLANTS. (FROM ISLEY, 1935.)

Food	Duration of larval stage		Eggs deposited at 25° C. and 28° C.	
	Days at 27° C.	No. larvae	Ave. number	Pairs
Corn ear	12.47 ± .05	139	1444.4	19
Corn ear and silk	13.49 ± .07	104	613.7	15
Cow peas	14.77 ± .02	26	960.0	4
Corn silks	15.18 ± .10	50	341.4	7
Alfalfa heads	16.35 ± .11	59	*372.5	23
Soybeans	16.44 ± .08	16	495.9	13
Alfalfa foliage	17.33 ± .07	73		
Cotton	18.25 ± .18	60	544.0	5
Tomato fruit and foliage ..	24.04 ± .32	24	†	
Tomato stems and foliage ..	24.97 ± .25	34		

* Alfalfa.
† At 22° C. on tomato, 183 eggs, av. for 6 pairs of moths.

rate of development, being highest on those developing slowly. The number of eggs deposited by females reared on the different foods was also roughly parallel with the rate of development, being greatest for those developing more quickly.

Insects of More Restricted Food Habits

Among insects of more restricted food habits three or four cases may be mentioned in which closely related species of plants differ in their availability as utilizable food for an insect.

Wadley (1931) found that although the green bug (*Toxoptera graminum*) could maintain colonies indefinitely on wheat (*Triticum vulgare*), rearing was somewhat difficult on Mindum durum (*Triticum durum*). There was about 50 per cent. mortality on this variety. On Vernal emmer (*Triticum dicoccum*) less than 10 per cent. of the aphids matured and no second generation developed. The interspecific wheat hybrids which have been recently bred by agronomists and plant breeders might prove a fertile field for study of resistance to this insect.

Since the middle of the last century it has been known that the grape *Phylloxera* was unable to maintain colonies on certain species of *Vitis*. This resistance reaction is still unchanged (Husmann, 1930), and apparently depends on some feature in connection with food of the insect. It has been shown to be due to a dominant genetic character in the plant.

French workers (B. Trouvelot *et al.*, 1933) have found recently that wide differences exist in the ability of the Colorado potato beetle (*Leptinotarsa decemlineata*) to develop and maintain a population on various species of the genera *Solanum, Datura* and *Nicotiana*. Notable differences in susceptibility to the attacks of the beetle were observed among tuber-bearing species and varieties of *Solanum*. A few species of *Solanum* were abandoned by the insects without tasting, on others there was little feeding but no growth, on still others the larvae lived various lengths of time but died before maturing.

Smith (1921) has found differences in various phases of the biology of the boll weevil when reared under similar conditions on Upland and on Sea Island cotton.

INSECTS OF RESTRICTED HABITS IN WHICH THE FOOD DIFFERS AMONG PLANTS WITHIN THE HOST SPECIES

In the study of varieties resistant to insect attack several cases have been studied in which varieties or individual plants would not support a population of an insect. These cases involve variation within a host species and are of especial interest because the inheritance of this reaction may be more easily studied.

More than 100 years ago (Lindley, 1831) an apple variety, Winter Majetin, was first reported as resistant to the woolly apple aphis (*Eriosoma lanigerum*). From time to time other varieties have also been observed to show this character, and all have retained them according to recent experimental work. Le Pelley (1927) in a study of Northern Spy apple was never able to get the woolly apple aphis to reproduce on this variety, although they would feed on it for as long as five weeks. No trace of galls was evident, and colonies placed on either roots or stems eventually died out. The same facts were true of Winter Majetin. The Northern Spy variety appears to carry this character in the heterozygous condition as some of the progeny are susceptible.

DeLong and Jones (1926) working with the Houghton gooseberry aphid (*Myzus houghtonensis*) found certain plants of the Houghton variety on which the insects would feed but on which they were unable to maintain a population. The plants were indistinguishable from susceptible ones typical of the variety.

In his study of the raspberry aphids, Winter (1929) found fewer individuals of *Amphorophora rubi* in the field on the Herbert variety than on any other. Under cage conditions the aphids in colonies increased at a much slower rate on this variety than on others studied and eventually died out. He concluded from further experiments that the thickness of cuticle was not a limiting factor and that difference in food material used by the aphids possibly accounted for the resistance of the Herbert variety.

Blanchard and Dudley (1934), working independently in California and Wisconsin, have found individual plants of several varieties of alfalfa on which the pea aphid (*Illinoia pisi*) was unable to maintain a population. Progeny of these same plants showed similar resistance, indicating the inheritance of the character. Similar resistant individual plants have been found in Kansas in a number of varieties (Painter and Grandfield, 1935). Studies since the latter publication have indicated the inability of aphids to maintain a population on these resistant plants and on some of their progeny. These studies have been carried on by Mr. R. C. Dahms under the direction of the author. Typical data are presented in Table III.

The method used was to cage 5 last instar nymphs or adults on individual branches in Cellophane cages. At the end of 10 days the numbers of live and dead aphids were recorded. Two or three cages were usually placed on a plant at the same time. An interesting development of this series of experiments, which has a bearing on the subject of food, concerns the relative development of aphids on flowering and vegetative branches of the same plant. In a series of experiments, aphids were caged on paired branches of the two types on a number of individual plants that were more or less resistant. In every case there was a greater increase in the average number of aphids per parent among those feeding on the flowering branches. The difference in the averages between vegetative and flowering branches on the individual plants varied from 25.4 to 1.2 aphids per parent as the increase during a 10-day period. That differences exist in the composition of flowering or fruiting branches on various plants as compared to vegetative ones is fairly well known. The difference in the development of the aphids on the two types of branches and on the individual plants appears due to differences in food available to the insects.

Dahms, Shelling and Fenton (1936) have found considerable differences in the mortality of nymphs and length of life of female chinch bugs fed on different varieties of

TABLE III

EXAMPLES OF DIFFERENT RATES OF POPULATION INCREASE OF PEA APHIDS ON DIFFERENT PLANTS OF ALFALFA AND ON DIFFERENT BRANCHES OF THE SAME PLANT

Plant No.*	Temp. approx.	No. of parental aphids	Adults		Nymphs		Ave. increase per aphid in 10 days	Remarks
			Dead	Alive	Dead	Alive		
3	Various	95	35	143	62	1008	11.6	Count of dead adults not made in one set of tests.
5	Various	85	69	1	34	3	.035	
5 different " } mostly R	78°	30	11	24	2	222	7.4	Flowering branches.
" }	78°	30	22	3	36	16	.53	Vegetative branches.
1–2S21–2E	78°	5	3	2	0	8	1.8	Flowering branches.
"	78°	5	5	0	11	3	.6	Vegetative branches.
1–3S1–4–8	78°	5	0	14	0	132	26.4	Flowering branches.
"	78°	5	3	2	4	5	1.0	Vegetative branches.

* The contrasting pairs of tests were run simultaneously under similar conditions.

sorghum. They have also found differences in the number of eggs laid. Females of the over-wintering generation fed on Atlas sorgo laid an average of 4.3 eggs during an average span of life of 8.5 days. Those fed on Dwarf Yellow Milo laid an average of 73.4 eggs during an average length of life of 23 days. The mortality of nymphs after the first instar averaged 8 per cent. when reared on Dwarf Yellow Milo as compared to 84 per cent. on Atlas. Insects reared on Atlas were smaller. These differences in life history appear to be only a part of the mechanism of resistance to chinch bug attack among the sorghums.

Several genetic factors and several causative factors appear to be involved in the resistance of various varieties of wheat to the Hessian fly. (Painter, Salmon and Parker, 1931). The relative ability of larvae to commence feeding on the resistant varieties must frequently be considered. The food of these larvae is extracted largely or wholly through the unbroken cell wall of the plants.[4] The difference between varieties, therefore, may be a difference in the permeability of the cell walls to enzymes of the insect or to partially digested food material. It may differ in this respect from the cases of the Homoptera cited above.

Discussion

Most of the examples cited confirm the view that varieties or species of plants which the insects eat do not all serve equally well for food when measured by the maintenance of the insect population. There are some instances in which various parts of the same plant have given similar differences in respect to insect nutrition. In those cases which have been studied this difference in food is visible chiefly in its effect on *length of life, death rate, size* and *fecundity,* singly or in combination. The *life span* may be lengthened or shortened, depending on various environmental factors such as temperature, as well as the insect and plant involved. When fed on resistant plants, the life of the insect usually is shortened and

[4] See discussion by Painter, *Jour. Econ. Ent.,* 23: 320–321, 1930.

death most frequently takes place either in the first instar or at about the time the insect reaches the adult stage. There are relatively few cases (Isley, 1935) in which actual measurements of *size* have been made, but occasionally mention is made that insects reared on resistant plants were smaller than those on susceptible ones. *Fecundity* was noted by Isley in the study of the corn-ear worm, for he called attention to the greatly reduced oviposition of the moths reared on the less usable food plants. In the studies of aphids, no progeny counts have been recorded for individual females, but since colonies were not maintained on resistant plants, reduced fecundity undoubtedly occurred. In the case of the pea aphid on alfalfa there were usually fewer nymphs recorded from adults on resistant plants, and these usually died while small.

There are several suggested explanations of these differences in effects of food observed with the insects and plants mentioned. *Specific poisons* are not uncommon among plants and may be the basis of some of the differences. There are two groups of facts, however, that tend to make such a possibility less likely. One of these is that the insects frequently feed for a period of time and occasionally mature on the resistant plants. The other is that such factors as reduced size and fecundity would not appear to be the result of poisons.

The varying *availability of food* as a whole may be partial explanation in some cases, particularly that of the Hessian fly. Uvarov (1928) points out that all digestible elements of plant cells are included within cell membranes, usually of cellulose, and that the problem of extracting this food must be solved by insects. Hemiptera have solved the problem, partially, by puncturing the cells. Nevertheless, the various insect species differ greatly in respect to the amount of injury done and in the transfer from plant cell to plant cell of the enzymes injected by the Hemipteron. This is a case of relative permeability of the cell walls to the enzymes involved or of inactivation of enzymes by living plant cells. Varieties and species

of plants may differ in respect to these reactions which thus furnish a basis for resistance.

Related to the availability of food is the possible *lack of specific food materials,* especially proteins, in species or varieties of plants. Differences in varieties with respect to chemicals, especially pigments and, to some extent, proteins, have been frequently noted and their inheritance described. The development of insects with respect to specific food substances or mineral elements is almost an untouched field, but cases are known where specific substances play an important part in insect metabolism.

While *vitamins* in insect nutrition have been studied very little, enough has been done to demonstrate their importance in some cases of insect metabolism. Likewise, differences in vitamin content have been shown to exist among varieties of plants. In expecting an insect to do equally well on two varieties of a plant we may, figuratively speaking, be expecting our live stock to do as well on white as on yellow corn. This does not necessarily mean that the same vitamins affect both insects and warm-blooded animals. Substances analogous to vitamins may be the basis of some cases of resistance.

In addition to differences in the kind of food materials available to insects in various species and varieties of food plants, there may be present actual *differences in the quantity.* It has been suggested (Uvarov, 1928) that the excretion of honeydew by aphids results from the necessity of ingesting more carbohydrates from the sap of plants than are needed by the insect, in order to get a sufficient amount of the scanty supply of proteins available there. This may be the explanation for the increased reproduction of the pea aphid on flowering stems as compared to that on vegetative branches of alfalfa plants and perhaps of differences between individual plants.

By thus analyzing the possible factors involved, it should be easier to plan experiments which will confirm or reject the suggested explanations. As data accumulate, it may become necessary to add to or subtract from

the list of factors given and to be more definite in their statement. The explanations suggested above probably have their basis in differences in the protoplasm or cell contents of individual plant cells. It appears that such differences play an important rôle in the resistance of plants to insect attack.

CONCLUSIONS

The *actual* nutritive substances used by phytophagous insects in contrast to the plant parts which insects *eat* is a factor of great importance in insect biology and deserves as thorough and accurate a study as that which has been given to humidity and temperature. Mere lists of plants on which insects feed is only a small start on the problem. At present, the only available measure of the food value of a plant to an insect is the rate and extent of insect development, and this value differs even within plant varieties.

Where differences in varieties exist, studies of insect biology made without knowledge of, and exact statement of, the variety of plant involved may have to be repeated. Lack of such information puts the study in the same class with those made without authoritative identification of the insect involved.

The comparative availability of different species of food plants has been shown to have an important effect on the relative abundance of insect pests. Plants also influence the incidence and effectiveness of insect parasitism through their effect on death rate and fecundity. Thus the influence of even a low level of insect resistance in plants may assume greater importance than is evident from small experimental plots.

Workers are just beginning to realize the rôle that food may play in the factors causing resistance. Often various morphological or growth characters of plants were mentioned as the cause of resistance in certain instances and subsequent investigation showed that other factors were of greater or equal importance. Food relationships also may be involved in these cases, and it is believed that further studies will reveal their connection with many cases of resistance.

The utilization of differences in food value in varieties of plants may furnish us with a tool for the study of phases of insect nutrition. There is evidence that varieties may be developed differing chiefly in the character causing resistance through food relationships. Chemical or biological analysis of such varieties may throw more light on the real food of phytophagous insects.

Underlying the interrelations of insect and plant as discussed in the preceding paragraphs, there is involved the whole evolution of the plant-insect relationship, based primarily on food. Progress has been made in the analysis of the evolution of morphological structures of insects, but this must have been accompanied by similar evolution in physiological reaction, especially in respect to food. The accumulating evidence of the presence of biological races of insects, so-called "physiological species," differing in food habits, is evidence that the evolution of plant and insect relationships has been parallel. The contributions of resistance studies to this field have hardly begun, but we may expect them to be considerable.

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REVERSAL OF SYMMETRY IN *CAMPELOMA RUFUM*, A FRESH-WATER SNAIL[1]

PROFESSOR HARLEY J. VAN CLEAVE
UNIVERSITY OF ILLINOIS

MOST of the published studies on the occurrence of reversal of symmetry in snails have been concerned with egg-laying fresh-water pulmonates. Members of the family Viviparidae give particularly favorable conditions for observing reversal of symmetry, since the young snails are carried in the maternal uterus until the shell is fully formed. In a series of life history studies on the members of this family, *Campeloma rufum* has been the object of intensive study over a period of years. The writer expresses appreciation to Dorothy A. Altringer, who was associated in this study during the year 1931–32. All the material incorporated in this study came from the Salt Fork River at Homer Park, Illinois.

Evidences presented in the present paper indicate that reversal of symmetry in *Campeloma rufum* does not conform to a simple Mendelian behavior. Individuals with reversed shells rarely attain bearing age. Progressive reduction of numbers of reversed shells from uterine stages to maturity suggests the possibility that shell reversal may be associated with some type of lethal factors.

Normally, in *Campeloma*, the shell is coiled in a right-handed spiral so that when the snail is crawling the aperture through which the body extrudes lies to the right of the axis of the shell. This typical form of the shell is termed dextral. Occasionally, a sinistral individual is found, in which the shell is coiled to the left. In *Campeloma*, reversal of symmetry has been regarded as so unusual that the discovery of sinistral shells has been considered of enough importance to merit recording in the literature. Call (1880: 207 and 1886: 165), Baker

[1] Contribution from the Zoological Laboratory of the University of Illinois, No. 487.

(1928:60) and Hand (1928:106) have commented upon the infrequency of reversed shells in the various species of *Campeloma,* but only incidental observations on reversal have ever been published. Therefore, particular attention has been directed to reversal of symmetry in this study.

As early as 1880, Call (p. 207) referred to a contrast between free and uterine shells in regard to the frequency of occurrence of sinistrality. For *Campeloma rufum,* Call found 1.5 per cent. of the uterine shells sinistral and only about one tenth of one per cent. of the adult shells. His observations were made on collections from New York state and consequently give evidence that the observations recorded in the present paper are not local phenomena.

In the early months of the present investigation, accurate records of the occurrence of sinistrality were not always kept. Consequently not all the collections studied have been used in the following tabulations. Careful records were kept for a total of 1,355 individuals of *C. rufum* taken from the area under consideration. As shown in Table I, these collections represented all seasons of the year. A total of fourteen sinistral shells was found. This gives an incidence of 1.03 per cent. of sinistrality in the free living snails taken from the Salt Fork,

TABLE I

THE OCCURRENCE OF SINISTRALITY IN SHELLS OF *Campeloma rufum* FROM THE SALT FORK RIVER

Date of collection	Total shells observed	Number of sinistral shells
Aug. 13, '32	62	2
Sept. 1, '33	237	1
Sept. 5, '32	208	5
Sept. 29, '31	166	1
Oct. 21, '33	53	0
Oct. 25, '31	67	0
Jan. 13, '34	51	0
Mar. 3, '34	25	1
Apr. 15, '34	146	0
Apr. 23, '32	91	0
May 15, '32	78	2
May 19, '34	171	2
Totals	1,355	14

Incidence of sinistrality in stream population 1.03 per cent.

far exceeding the record of one tenth of one per cent. recorded for this species by Call.

TABLE II

THE OCCURRENCE OF SINISTRALITY IN THE UTERINE YOUNG OF *Campeloma rufum* FROM ADULTS TAKEN FROM THE SALT FORK RIVER

Date of collection	Number of uteri examined	Total number embryonic young	Number of dextrals	Number of sinistrals
Sept. 1, '33	14	50	40	10
Sept. 5, '32	65	115	111	4
Sept. 29, '31	15	509	493	16
Sept. 30, '30	10	198	192	6
Oct. 21, '33	43	156	145	11
Oct. 25, '31	21	208	194	14
Mar. 3, '34	25	164	155	9
Apr. 15, '34	26	291	268	23
Apr. 23, '32	21	79	67	12
May 19, '34	56	88	83	5
June 4, '32	24	1	1	0
June 25, '32	50	23	21	2
Aug. 13, '32	19	39	39	0
Totals	389	1,921	1,809	112

Incidence of sinistrality in uterine young 5.83 per cent.

A preliminary examination of the uterine young gave evidence that sinistrality is not uncommonly encountered in the unborn young carried in the maternal uterus. The impression that these occur in greater numbers than ordinarily supposed and in excess of the 1.5 per cent. recorded by Call (1886) led to a careful check of this matter. Out of the numerous individuals examined in this study, complete data are available for the uterine contents of 389 parent individuals. In Table III the symmetry of the uterine shells is analyzed.

A comparison of Tables I and II shows that reversal of shell symmetry occurs more than five times as frequently in uterine shells as in the free living population. For both of these groups the percentage of sinistrality found in this study far exceeds that reported by Call (1880:207). Individual samples, even from the same habitat, vary so greatly that the figure representing incidence of sinistrality could be greatly modified by selecting certain samples. Thus, the collection of September 29, 1931, gave a sample of uterine young in which only slightly more than 3 per cent. were sinistral, though

in a small sample collected on September 1, 1933, 20 per cent. of the uterine young were reversed.

In examining the contents of maternal uteri, particular attention was paid to the condition of the reversed young shells in the expectation that some means of explaining the differential between incidence of sinistrality in free and unborn individuals might be discovered. No disintegrating bodies or empty shells were found in any of the uterine sinistrals. There is no evidence of reduction in numbers of sinistrals during the stay in the maternal uterus. The differential in incidence is thus established after birth. In the period of free existence there are effective factors operating to eliminate the sinistral individuals. Either these are in the nature of hereditary factors, probably lethal genes, or they may be in the nature of limitations to normal physiological activity and growth accompanying the morphological pattern of sinistrality in this species. The transposition of parts of the body and suppression of some of the normally bilateral organs in embryonic development of the Streptoneura might readily provide a basis for morphological maladjustment of parts in the individuals showing reversal of the normal symmetry. These maladjustments might readily render the disturbed organs inadequate to care for the physiological demands of the individual. Under such conditions the elimination would be progressive. In the field and laboratory study of this problem it has been clearly demonstrated that reduction in numbers of sinistral shells is progressive.

From facts presented in Table III, it is obvious that not one of the sinistrals has attained a size that would put it in an age class of more than one year. An initial incidence of 5.83 per cent. of sinistrality in the uterine young becomes reduced to 1.03 per cent. in the total free living population. When the latter figure is still further analyzed it becomes apparent that sinistrals are wholly lacking in the portion of the population which is more than one year of age. Since the 1.03 per cent. was calculated on

the basis of the entire free population, the actual incidence in the individuals under one year of age would be almost doubled.

TABLE III

AN ANALYSIS OF THE UTERINE CONTENTS OF TWELVE FREE LIVING SINISTRALS OF *Campeloma rufum* TAKEN FROM THE SALT FORK RIVER

Date of collection	Height of shell in mm	Uterine contents		
		Number of eggs	Height of embryonic shells in mm	
			Dextrals	Sinistrals
Aug. 13, '32 ...	15.6	4	0	0
" ...	15.5	0	0	0
Sept. 1, '33 ...	16.6	0	0	0
Sept. 5, '32 ...	15.7	0	0	0
" ...	14.9	0	0	0
" ...	14.3	0	0	0
" ...	17.0	0	0	0
" ...	13.4	0	0	0
Sept. 29, '31 ...	18.3	0	2.84	0
March 3, '34 ...	23.5	0	3.47	3.57
" ...			3.37	
" ...			3.57	
" ...			3.68	
May 19, '34 ...	19.8	1	0	0
" ...	22.0	7	0	0

There is a fairly large body of literature dealing with various aspects of the reversal of symmetry in snails. In the older literature, attempts to discover the cause of reversal are wholly inadequate. Call (1880: 208) sought to explain the occurrence of reversed symmetry as the simple mechanical effect of crowding in the maternal uterus. He invoked this as the explanation for all types of abnormality found in the uterine young. Wilson, in "The Cell" (1925) has reviewed the literature dealing with the correlation of bodily symmetry in snails and the position of the spindle in the early cleavages of the egg. On this basis, cytological explanation of reversal has been offered in the works of Crampton (1894), Conklin (1897), Kofoid (1895), Holmes (1899) and of other students of gastropod embryology. In recent years attention has been directed not alone to the cytological basis for establishing reversal but even more sharply to the inheritance of symmetry. Sinnott and Dunn (1932: 305), quoting from works on pulmonate snails, state that in its inheritance the reversal of symmetry in snails acts as a "clear

case of the effect of a single gene on the earliest stages of development." It had previously been shown by Conklin, Crampton and others, as cited above, that the direction of coiling of the shell is determined by the direction of the tilt of the spindle during the second (and possibly the first) cleavage stage. Since the position of the spindle bears a definite relationship to the orientation of the egg in the maternal ovary before maturation, the type of symmetry is not determined by the hereditary constitution of the egg itself but rather by conditions imposed upon the egg by the mother.

In commenting upon this maternal influence, Boycott, Diver, Garstang and Turner (1933: 127) in their work on *Limnaea peregra* remark that "sinistrality behaves as a Mendelian recessive character, but the appearance of any change of twist imposed by crossing is delayed by one generation and segregation occurs in F3."

It should be called to mind that the definite operation of genetic behavior for sinistrality in the pulmonate snails gives no evidence of the presence of lethal factors or of progressive elimination of the sinistrals as discussed for *Campeloma rufum.*

So far, the writer has been unable to rear *Campeloma rufum* in the laboratory. Hence controlled breeding experiments have not been possible. The only information concerning the behavior of sinistrality has been gleaned from laboratory analysis of snails produced in nature. The observed facts give strong evidence that lethal factors accompany the conditions which lead to the production of sinistrality in *Campeloma rufum.* In the operation of this lethal factor not all sinistral individuals are eliminated at the same stage of development. There is thus a progressive elimination of the sinistrals, extremely small numbers of which ever reach the age of one year. In an extension of this concept of lethal genes it seems plausible that the length of life of individuals in species having a definite life span may be determined by hereditary mechanism.

SUMMARY

(1) About 1.03 per cent. of free living *Campeloma rufum* in the Salt Fork River at Homer Park, Illinois, have sinistral shells.

(2) Among uterine young about 5.83 per cent. are sinistral.

(3) After birth there is a differential death rate tending to eliminate the sinistrals before they reach an age of one year.

(4) Few sinistrals ever reach bearing age.

(5) Sinistrality in this species seems to be accompanied by lethal factors.

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OBSERVATIONS ON THE SPECIES RELATED TO *DROSOPHILA AFFINIS*, WITH DESCRIPTIONS OF SEVEN NEW FORMS

PROFESSOR A. H. STURTEVANT
AND
PROFESSOR TH. DOBZHANSKY
W. G. KERCKHOFF LABORATORIES, CALIFORNIA INSTITUTE OF TECHNOLOGY

INTRODUCTION

Drosophila affinis Sturtevant (1916, p. 334) has been recorded from many localities, ranging from New Hampshire and Illinois, south to Florida and west to Texas and Kansas (Sturtevant, 1921). We find that there are forms in Alaska, the northwestern United States and the Mexican plateau that also will fit the published descriptions of affinis; but these represent distinct species, and careful study shows that the original material is itself a mixture of several species. The members of this group are clearly closely related to the forms that have gone under the name of *Drosophila obscura*. This is also a complex group, containing at least four European species and the western American *Drosophila pseudoobscura* (Frolowa and Astaurow, 1929) and *Drosophila miranda* (Dobzhansky, 1935).

KEY FOR PINNED MALES OF THE SPECIES OF AFFINIS GROUP

The key given herewith is to be taken as an expansion of the first line of couplet 4 in the key given by Sturtevant (1921, p. 67), or of the first line of couplet 5 in that given by Malloch and McAtee (1924, p. 34). The descriptions of the species include only those respects in which they differ. For other characters, common to all of them, see the descriptions cited.

It should be added that all members of the group have a single tooth of a second sex-comb (Fig. 1) on the second tarsal segment, where there is a fully developed comb in members of the obscura group. We have found no differences among the eight forms in the internal genital ap-

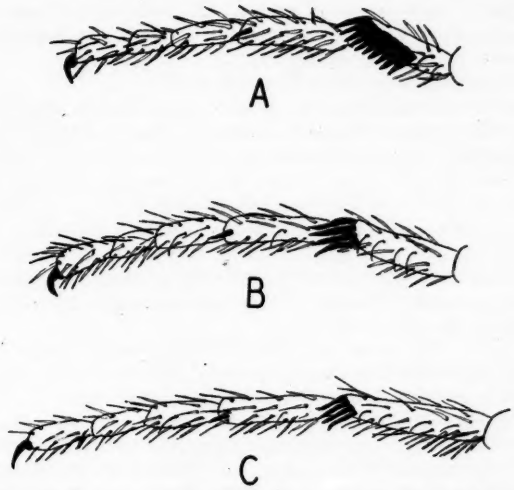

FIG. 1. Tarsi of A– *Drosophila algonquin*, B– *D. affinis* and C– *D. athabasca.*

paratus of either sex, while all of them have spiral testes different from the ellipscidal ones present in species of the obscura group.

1. Sex-combs with 8–10 teeth, nearly parallel to axis of the tarsal segment; large species, more brownish than others ..... **algonquin**
– Sex-combs with 4–6 teeth, more oblique 2
2. Frons slightly pollinose when viewed laterally; sex-combs short 3
– Frons scarcely pollinose 4
3. Frons not pollinose when viewed from vertex; mesonotum not uniformly pollinose, with indistinct longitudinal stripes ..... **seminole**
– Frons pollinose when viewed from vertex; mesonotum uniformly pollinose ..... **narragansett**
4. Sex-combs longer (Fig. 1B) ..... **affinis**
– Sex-combs shorter (Fig. 1C) 5
5. Mesonotum with four relatively distinct longitudinal less pollinose stripes (two inside and two outside the dorsocentral lines) ..... **azteca**
– Mesonotum with two relatively less distinct dark longitudinal stripes (inside the dorsocentral lines) 6
6. Legs distinctly brownish ..... **athabasca**
– Legs wholly yellow ..... **mahican**

DESCRIPTION OF SPECIES

Drosophila algonquin, sp. n.

♂. Frons dull, light brown. Mesonotum light brown, indistinctly longitudinally striped. Legs yellow; sex-combs with 8 to 10 teeth (Fig. 1A), larger

than in affinis. Male genitalia (Fig. 2A) with a short and broad eighth sternite and a blunt distal end of the penis. The anterior margin of the eighth sternite rounded and not thickened.

♀. Abdomen indistinctly banded.

Distribution. Massachusetts: Woods Hole (type locality), East Falmouth, Waquoit; New Jersey: Mendham, Sparta; Michigan: Detroit; Indiana: North Manchester; Illinois: Flat Rock.

Drosophila affinis Sturtevant

♂. Frons dull brown. Mesonotum brown, with faint indications of longitudinal stripes anteriorly. Legs yellow; 4 to 6 teeth per sex-comb (Fig. 1B). Medium size. Genitalia (Fig. 2B) with an elongate eighth sternite whose anterior margin is not thickened. Penis acuminate.

♀. Abdomen distinctly banded.

Distribution. New Jersey: Morristown (one specimen); South Carolina: Greenville; Florida: St. Augustine, Lakeland; Alabama: Kushla (type locality); Louisiana: Baton Rouge; Texas: Houston, Florence.

Duda (1927, p. 135) has recorded D. affinis from Paraguay. This record requires confirmation, since experience shows that this author sometimes misinterprets American locality labels; if a member of the present group occurs so far south, we can only suggest that azteca or an undescribed form may be concerned.

Drosophila affinis subsp. *iroquois*, subp. n.

Differing from the typical affinis in that it has darker frons, mesonotum, and pleurae. Legs somewhat brownish, especially apices of femora and bases of tibiae.

Distribution. Massachusetts: Woods Hole (type locality); New York: Staten Island; New Jersey: Fort Lee, Sparta, Mendham, New Brunswick; Mississippi: Agricultural College (1 specimen).

Drosophila athabasca, sp. n.

♂. Frons dull, dark brown. Mesonotum dark brown, with a pair of faint longitudinal stripes just inside the dorsocentral lines. Legs yellow, apices of femora and bases of tibiae brown; sex-combs with four teeth, very small (Fig. 1C). Medium size. Genitalia (Fig. 2C) with an elongate eighth sternite thickened and blunt on its anterior margin.

♀. Abdominal banding indistinct.

Distribution. Alaska: Gravina Island (type locality), Ketchikan, Juneau, Chitina; British Columbia: Quesnel, 150-mile House, Pavilion, Lake Shuswap, Arrowhead, Nakusp, Kaslo, Campbell River, Lake Cowichan; Washington: Cape Flattery, Brinnon; Oregon: Reedsport; Wyoming: Grand Teton, East entrance to Yellowstone Nat. Park, Big Horn Mts., Sundance; South Dakota: Black Hills; Colorado: Cache la Poudre Canyon, Grand Lake, Estes Park, University Camp.

Drosophila athabasca subsp. *mahican*, subsp. n.

Differs from typical athabasca in somewhat paler frons and thorax; legs yellow, not brownish.

Distribution. New Hampshire: Hanover (type locality); Massachusetts: Middleboro, Woods Hole; New Jersey: Mendham.

Drosophila azteca, sp. n.

♂. Frons dull, dark brown. Mesonotum dark brown, a relatively darker shining longitudinal line just inside each dorsocentral row, and a similar but less distinct and narrower line lateral to each dorsocentral row. Legs yellow, slightly brownish; sex-combs with 4 to 5 teeth, small. Size medium. Genitalia (Fig. 2D) with eighth sternite thickened and acuminate on the anterior margin. Penis acum'nate.

♀. Abdominal banding indistinct.

Distribution. Oaxaca: Cerro San Jose (type locality); Morelos: mountains north of Cuernavaca; Durango: Otinapa, Aserraderos.

Drosophila seminole, sp. n.

♂. Frons brown, paler anteriorly; strongly pollinose when viewed laterally but not when viewed from vertex. Mesonotum brown, with indistinct longitudinal stripes. Legs yellow; sex-combs as in athabasca or azteca. Medium size. Genitalia unknown.

♀. Abdominal banding indistinct. Frons not pollinose.

Distribution. Alabama, Mobile County: Kushla (type locality), Whistler.

Drosophila narragansett, sp. n.

♂. Frons strongly pollinose when viewed either laterally or from vertex. Mesonotum brown, grayish dusted, longitudinal stripes faint or absent. Legs yellow, slightly brownish; sex-combs small, similar to those of athabasca or azteca. Somewhat smaller than affinis. Genita'ia (Fig. 2E) with the eighth sternite smoothly rounded on the margin.

♀. Frons not pollinose.

Distribution. Massachusetts: Woods Hole (type locality); Connecticut: Darien.

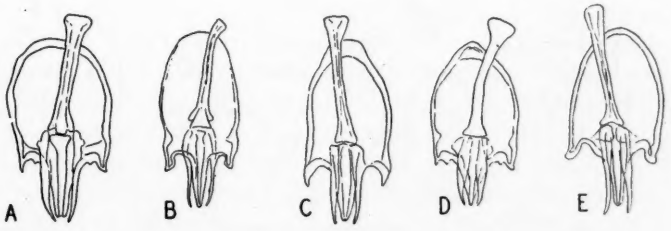

FIG. 2. The eighth abdominal sternite and the penis apparatus of A– *Drosophila algonquin*, B– *D. affinis*, C– *D. athabasca*, D– *D. azteca*, E– *D. narragansett*.

The types of all the species and subspecies here described are deposited in the American Museum of Natural

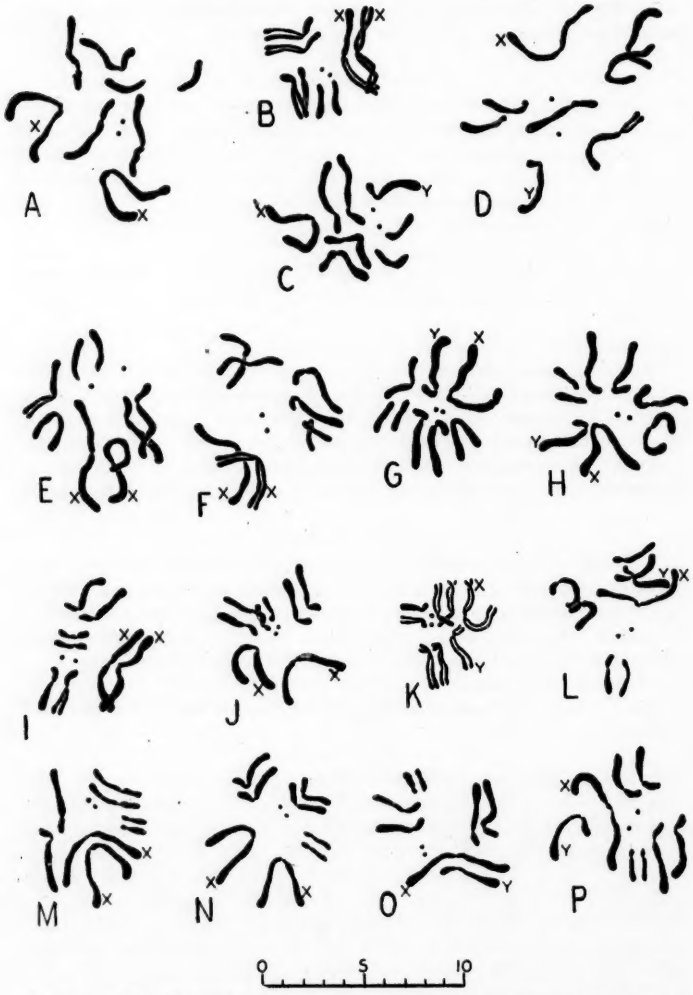

FIG. 3. Metaphase plates in the cells of the larval nerve ganglia in A and B– *Drosophila algonquin* females, C and D– *Drosophila algonquin* males; E and F— *D. affinis* females and G and H males; I and J— *D. athabasca* females and K and L males; M and N– *D. azteca* females and O and P males. X– the X-chromosome; Y– the Y-chromosome. The scale below represents 10 micra.

History, New York, which also contains the types of *affinis* and *miranda*.

Chromosomes

Metz (1916, A, C) found in *Drosophila affinis* five pairs of chromosomes. The X–chromosome is V–shaped and the Y is J–shaped. Among the four autosomes two have distinctly subterminal spindle fiber attachments, one, the shortest, is rod-shaped, and the fifth is very small, dot-like. Since among the species studied by Metz no other except affinis had a chromosomal group with such characteristics, he isolated it into a special "type K" containing affinis as the sole representative. At present we know, however, that at least six distinct species were confused under the name "affinis." We have studied the chromosomes of four of them (Fig. 3), using the acetocarmine smear preparations of the larval ganglia and picking out the division figures in the giant nerve cells. Comparing Metz's figures with ours, it seems most probable that the species he was dealing with was not the true affinis, but *Drosophila algonquin*.

All the species which we have studied have the essential characteristics of the type K of Metz. However, chromosomes of *Drosophila affinis* differ from those of its relatives in that one of its autosomes (Figs. 3 E–H) has a very nearly median spindle fiber attachment. In algonquin, athabasca and azteca the seemingly homologous chromosome has the fiber attachment in a distinctly subterminal position. *Drosophila athabasca* and *azteca* appear to have identical metaphase plate chromosomes (Figs. 3 I–P), but they differ from algonquin and the true affinis, since the shortest autosome has a subterminal fiber attachment instead of the apparently terminal one found in the latter two species. It must be mentioned, however, that this difference is reasonably clearly visible only in favorable plates: it is, for instance, not noticeable in the smaller nerve cells. Thus, among the four species of the affinis group studied cytologically three are distinguishable in the metaphase plate configurations.

No detailed study of the salivary gland chromosomes of the species of the affinis group has as yet been made. Preliminary information is available only on athabasca and azteca. In these the salivary gland nuclei contain five long and apparently three short strands attached to a common chromocenter. In males two of the long strands are pale. The provisional interpretation of this condition is as follows. The two long strands that are pale in the male are the two limbs of the X–chromosome. The remaining three long strands are the longer limbs of the autosomes having subterminal fiber attachments. The three short strands correspond—one to the dot-like autosome and two to the shorter limbs of the two autosomes in which the fiber attachment is clearly subterminal. The short limb of the autosome having more nearly terminal attachment (see above) is probably inert.

ECOLOGICAL DATA

Our collecting west of the Mississippi has been done almost exclusively by the use of trap bottles containing fermented banana, exposed in forested areas and examined for adult specimens at about sunset. Most of this collecting (all the records for azteca and athabasca) has been done by one of us (Dobzhansky). The collecting in the eastern United States has been done largely by Sturtevant, using the banana trap method and also (more extensively) sweeping tree trunks with a net and collecting individual specimens found on bleeding trees. These various methods do not appear to affect the relative frequencies of the species concerned.

At Woods Hole the commonest species of the group is iroquois, followed by algonquin and mahican, with narragansett very rare. In southern Alabama affinis is somewhat commoner than seminole. Professor J. T. Patterson informs us that in central Texas affinis is more frequent than pseudoobscura. In Alaska only athabasca was found, frequently in great abundance. The distribution of this form and of pseudoobscura overlap in the region from British Columbia to the Rocky Mountains of north-

ern Colorado, but in this overlapping zone athabasca is clearly commoner as one proceeds north and northeast, and pseudoobscura south and southwest. That is to say, one species replaces the other rather rapidly as one moves at right angles to the boundaries of their distribution. For instance, at Yale and Merritt, British Columbia, only pseudoobscura was found among large numbers of flies collected. Further north, at Pavilion, athabasca appeared as an admixture to the population consisting predominantly of pseudoobscura; near 150-mile House athabasca decidedly predominates, and near Quesnel a single pseudoobscura was found among a mass of athabasca. Occasional specimens of either species may, of

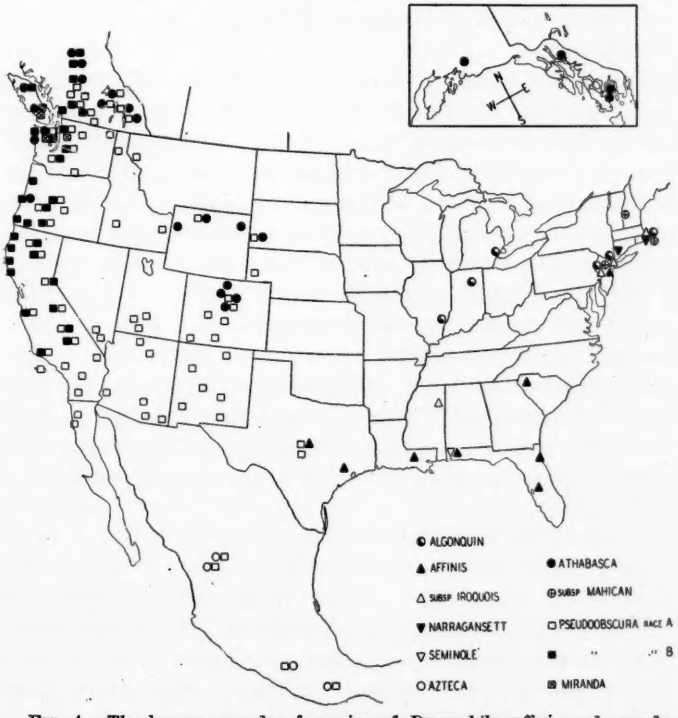

FIG. 4. The known records of species of *Drosophila affinis* and *pseudoobscura* groups. The insert map above represents a part of Alaska.

course, appear well within the range occupied by the other species—a single athabasca individual found at Reedsport, Oregon, does in fact represent such an isolated occurrence (Fig. 4). In the northern Rocky Mountains pseudoobscura is more frequent at lower elevations, and athabasca in the subalpine zone (although further south, at the tree line on Pike's Peak only pseudoobscura was found). All these facts suggest that athabasca and pseudoobscura are ecologically nearly equivalent. It does not appear from our present information that such a replacement in a relatively narrow zone occurs for any other species here discussed, but in many of the areas where this might happen we have little or no data. It may be surmised that when such data are available similar cases will be found, and also that additional species will be discovered.

Azteca and athabasca may be crossed (see below), and a number of facts indicate that they are very closely related. One is tempted to conclude that they have only recently diverged. In this connection it is of interest that the distribution areas of these two species are separated by a broad zone that is occupied exclusively by pseudoobscura, and as shown above pseudoobscura and athabasca do not seem to both survive in a given region (Fig. 4). The conclusion seems to be clear; azteca and athabasca were separated by an eastward extension of the range of pseudoobscura—a conclusion concerning the history of the latter species that is consistent with the results of studies now in progress, on the geographic distribution of inversions in the third chromosome of pseudoobscura.

INTERRELATIONS OF THE FORMS DESCRIBED

The eight forms concerned here are so similar in appearance that we have been unable to devise satisfactory methods of distinguishing pinned females. That the types listed as species are really distinct follows from laboratory experiments. We have kept strains of all of them at one time or another, and have made many attempts at interspecific crosses. Affinis (or iroquois—in most cases

both) has been tried with all the others; algonquin with narragansett, athabasca and azteca; seminole with mahican; and azteca with athabasca. With the exception of the last named, these crosses produce no offspring whatever. Affinis, algonquin, athabasca and azteca have also been tested with both races of pseudoobscura, with negative results.

In living material some differences not mentioned in the above descriptions are apparent. The females of affinis and algonquin have distinctly banded abdomens; in athabasca, azteca, seminole and mahican this banding is much less distinct, the pattern resembling that of pseudoobscura; narragansett has not been seen alive since this character was noted. Affinis, iroquois, algonquin and azteca are relatively easy to breed by the usual maize meal—molasses—agar technique, though more difficult than pseudoobscura; athabasca, mahican, seminole and narragansett are much more troublesome to maintain, and appear to be more sensitive to high temperature.

These facts leave no doubt that we are here concerned with "good" species. The relation of the two forms described as subspecies is less certain. Iroquois is only slightly different from affinis in color, and is fully fertile with it (strains from Texas, Alabama and Florida have been crossed to Woods Hole ones and have given fully fertile offspring of both sexes). However, since the variation is clearly a geographical one, it has seemed desirable to recognize and name the two types. Mahican and athabasca have not been compared in living material; but the only difference we can see is in color. Even the male genitalia are identical. It remains uncertain whether the range is a continuous one, since records are absent for the greater portion of the Canada-United States border, where they are needed for this purpose.

Drosophila azteca and *athabasca* may be crossed in either direction. Neither mating is as often successful as are matings within either species; that of athabasca ♀ × azteca ♂ is particularly difficult to obtain. All the

hybrids produced are sterile, and have rudimentary gonads. In the male hybrids the testis size is variable, apparently depending in part on which strains of the parent species are used (*cf.* the results of Dobzhansky and Boche, 1933, on the hybrids of the two races of pseudoobscura). In females the ovaries contain egg chambers only. All the females observed have been about the same size and proportions as the parent species, but all have had some macrochaetae markedly reduced in size. The males from the reciprocal crosses are strikingly different. Those from the azteca ♀ × athabasca ♂ are larger than their sisters or parents and have relatively very large wings of a characteristic shape. Those from athabasca ♀ × azteca ♂ are dwarfs, with relatively small wings; they are also much less numerous than their sisters on account of low viability. Neither type of males has reduced macrochaetae. The hybrid between azteca and athabasca is the fourth example of sterile hybrid in the genus Drosophila. The examples known previously are the melanogaster × simulans and the pseudoobscura × miranda hybrids. The hybrids between the A and B "races" of *Drosophila pseudoobscura* may be placed in the same category.

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SHORTER ARTICLES AND DISCUSSION

NATURAL HYBRIDIZATION AND GENETICS OF FLICKERS (*COLAPTES*)

On the North American Continent the two common species of *Colaptes,* a genus of the woodpecker family, are *C. auratus,* or the yellow-shafted flicker, and *C. cafer,* or red-shafted. That hybridization occurs on a grand scale between these two species was, according to Allen (1892), first pointed out by Baird in 1858. A very good account of the relationship between these two species is given in Allen's paper. The geographical area of active hybridization is given as extending from southeastern Texas northward along the western edge of the Plains into Canada and thence westward to the coast—a belt of country estimated from 300 to 400 miles wide and some 1,200 to 1,500 miles long. Recently Taverner (1934) gave a more detailed account of the geographical extent of hybridization in Canada based upon the collection ir the National Museum, Ottawa. This collection now consists of 166 flickers. Of these 115 specimens were collected from 21 localities westward of Manitoba to the coast, including Wood Buffalo Park, southern Alaska and Vancouver and Queen Charlotte Islands. Of these 60 are hybrids, 37 are red- and 18 yellow-shafted. The remaining 51, which are pure yellow-shafted, were collected from various localities eastward of the Saskatchewan-Manitoba boundary to the Atlantic. The present paper deals with a genetic study of these flickers and made on the suggestion and through the courteous assistance of Mr. P. A. Taverner.

The hybridization of these two species is of interest taxonomically because of the possibilities of the ultimate hybridization in some degree of the red-shafted species and the latent possibilities of subspeciation of hybrid types. Genetically they are of interest because they possess five contrasting plumage characteristics. Four of these are given in Table 1 for both species and hybrid together with the postulated genotypes. The fifth characteristic, namely, gray or brown crown plumage color, is not given because it did not appear to be a reliable characteristic in young birds.

The hybrid birds were classified by inspection according to the per cent. presence of yellow-shafted characteristics, with the exception of wing and tail color. The results are given in Tables 2 and 3. Table 2 consists of two families of hybrid parents and

TABLE 1

FOUR CHARACTERISTICS WITH POSTULATED GENOTYPES OF TWO SPECIES OF FLICKERS AND HYBRID

	Malar stripe (Males)	Wing and tail color	Throat color	Nuchal bar
Yellow-shafted	Black BBMMSS	Yellow YY	Fawn GGtt	Present NNAARR
Red-shafted	Red bbmmss	Red yy	Grey ggTT	Absent nnaabb
Hybrid	Black BbMmSs	Yellow Yy	50 per cent. Grey GgTt	100 per cent. Present NnAaRr

their young, collected in both cases just as the young had left their nest and were being fed by their parents. It is from these two families that the genetic interpretation is largely drawn. There is the remote possibility that at least one of the parents of each family might be a foster parent; however, the characteristics of parents and young would seem to discount this possibility.

TABLE 2

TWO FAMILIES OF HYBRID FLICKERS. THE TWO PARENTS ARE GIVEN FIRST, FOLLOWED WITH THEIR YOUNG NUMBERING FOUR AND FIVE RESPECTIVELY

Family No.	Sex	Malar stripe per cent. black	Wing and tail color	Throat color per cent. gray	Nuchal bar per cent. present
(1).....	♂	90	yel.	50	0
	♀	..	red	50	100
	♂	100	yel.	80	0
	♂	..	yel.	60	70
	♀	..	yel.	50	75
	♀	..	red	40	10
(2).....	♂	90	red	0	75
	♀	..	yel.	90	95
	♂	100	yel.	0	100
	♂	100	yel.	10	100
	♂	100	yel.	0	10
	♂	95	yel.	0	100
	♂	50	yel.	50	100

In Table 3 the other 47 hybrids are classified. Owing to the large proportion of males and also to the fact that the malar stripe is sex-limited, the birds were classified horizontally according to the per cent. presence of black-pigmented malar stripe and vertically according to the other three characteristics. The distribution and frequencies of the variates was the guide in arranging the classes. For the nuchal bar characteristic an arbitrary one per cent. class is given to indicate the number of variates possessing such a small trace of this trait. The discrepancy between

TABLE 3

CLASSIFICATION OF 47 HYBRID FLICKERS

Wing and tail color	Malar stripe ♂♂			Throat color					Nuchal bar				
Per cent. Black	No.	Red	Yel.	Per cent. gray				Fawn	Per cent. present				
				100	75–90	50–60	10–25	0	100	50–75	2–25	1	0
100 ..	8		8			5	2	1	6	1	1		
90 ..	2		2			2			2				
25–50 ..	4	2	2	1	2		1		1		3		
1 ..	4	4		2	1			1	1		1		2
0 (Red) .	19	16	3	13	3	2		1	3	3	5	6	2
♀♀	10	5	5	3	2	4	1		3	1	2	1	3
Total .	47	26	21	19	8	13	4	3	16	5	12	7	7

the higher per cent. value of one class and the lower of the next indicates that no variates fell within such values. With regard to the distribution of variates in Table 3, those classified horizontally as 100 per cent. black malar stripe are regarded as an F_1 type; those with 25 to 90 per cent. as F_2 segregants and the remainder of the males as back-cross types, that is, the progeny of hybrids × red-shafted.

The wing and tail colors refer to the shafts and under surfaces, although black pigment is also present in the vanes. The family data in Table 2 indicate that wing and tail color are the only pair of sharply contrasting characters and that yellow is a simple dominant to red, family 1 giving a perfect 3:1 ratio. However, 4 of the 26 hybrids classified as red in Table 3 were of an orange-red color. According to Allen, exceptional birds may possess any blend of red and yellow and individual quills in the same bird may vary from red to yellow. In our sample the quills of any particular bird were all of the same color. Whether this blending in occasional birds is of a genetic or environmental nature can not be determined from these data. Conceivably, the orange shade might be due to the fading of yellow pigment before the moult in heterozygous birds, the new feathers coming in yellow again.

The malar stripe or mustache receives its characteristic color from the distal half of the feathers, the basal half being dark-colored in both species. According to Allen, the malar stripe in adult yellow-shafted is limited to males, but in the young it may be present in both sexes. Ridgway (1914) describes it as wanting or much less distinct in young females. In our sample a few fawn-tipped feathers were present among the black or dark ones

in the occasional young bird. In red-shafted females the malar stripe region has usually a brownish tinge.

Black pigmented malar stripe is interpreted as being completely dominant to red. That there are more than one pair of factors involved is evident from the classes given in Table 3. The malar stripe of birds classified from 25 to 50 per cent. black have black and red feathers interspersed. The 90 and one per cent. classes have respectively a small and large proportion of red feathers. The postulated genotype is that one pair of factors (BB) exhibiting dominance are responsible for the presence of black pigment in the malar stripe of yellow-shafted and that the red-shafted have two principal pairs of recessive factors (mmss) which almost restrict the expression of the black factor when present. Thus the F_1, BbMmSs, are black, BbmmSs, 90 per cent. black, BbMmss, 25 to 50 per cent. black and Bbmmss, one per cent. black. There are other possibilities, for example, the effect of restriction factors on homozygous black, which can not be determined from these data. The factor for red wing and tail color appears to modify black malar stripe to some extent. Thus some variates classified as possessing respectively 25, 50 and 90 per cent. black malar stripe have red wings and tails.

In throat color both parents of family 1 are 50 per cent. gray and their four offspring range from 40 to 80 per cent. gray, suggesting a blending type of inheritance. In family 2 a fawn × 90 per cent. gray gave three fawns and two with 10 and 50 per cent. respectively gray color. From these results it is postulated that one pair of incompletely dominant factors (GG) are responsible for the expression of gray pigment in the red-shafted and that one principal pair of partially dominant restriction factors (TT) are present in the yellow-shafted species. Thus, the 90 per cent. grays and just under would have the genotype Ggtt, 50 per cent. GgTt and 10 per cent. and just over GgTT. On this factorial basis the genotypes GGTT would be expected to show fawn color. However, it is quite probable that several minor modifiers are present, since both gray and fawn colors themselves are clearly modified black and red, respectively. Moreover, the red-shafted usually possess a fringe of fawn-colored feathers between the gray throat and black breast feathers. Of the 47 hybrids it can be noted that only three are classified as having fawn-colored throats, due to the sample being largely drawn from the progeny of hybrids × red-shafted.

The nuchal bar characteristic is a semi-circular bar of red-tipped feathers around the nape of the neck. In young birds the crown feathers are also red or reddish tipped. Indications are that the nuchal bar is completely dominant to its absence. Family 1 would indicate that there is one pair of factors responsible for its expression together with some recessive restriction factors. A similar genotype complex is therefore given the nuchal bar characteristics, as that for malar stripe, namely, one pair of factors (NN) responsible for its expression in the yellow-shafted and two pairs of recessive restriction factors (aarr) in red-shafted. However, the distribution in Table 3 would suggest the presence of more than one pair of factors responsible for its expression. The nuchal bar characteristic is present in many species of woodpeckers in varied and complex patterns. The red-shafted species might therefore have it as a fundamental pattern but restricted from expression by recessive factors. On this assumption pure red-shafted could occasionally exhibit a trace of nuchal bar as a result of environmental influence overcoming the threshold of restrictive influence. However, the presence of traces of nuchal bar in red-shafted is regarded as evidence of hybridity. It is quite apparent that controlled hybridization experiments would be necessary to clarify the complicated factor interaction of this and the other characteristics.

None of the characteristics appear to be linked. However, the nature of the sample and complexity of the characteristics serve to obscure any linkage relationship that might exist. The four variates classified as having 25 to 50 per cent. black malar stripe are equally divided between red and yellow wing and tail colors, suggesting no linkage between these two characteristics.

The question arises as to the specific status of these two species. It is clear that the differences between them are preponderantly of a qualitative nature, while quantitative, morphological or physiological differences are of little or no account. Some slight geographical variations do occur, descriptions of which are given by Allen. Ridgway lists 3 red-shafted subspecies and 4 yellow-shafted. Some differences affecting mating may occur. The sample indicates that hybrid flickers have a preference for the red-shafted species. However, since the yellow-shafted species is dominant in all characteristics except the fawn-colored throat, the hybrids crossing with this species would give progeny 50 per cent. of which would be indistinguishable from pure yellow-shafted.

Other red-shafted characteristics would appear only when the hybrids mated. It can be noted that the hybrid parents of family 2 gave young which are predominantly of the yellow-shafted type.

Taxonomically, some confusion is likely to occur, due to mutations or hybridization, as among the flickers, when the criterion of specific status is largely that of plumage color. A review of the various species criteria and a discussion of the species problem are given by Robson (1928). In this sample of flickers are seen the possibilities through segregation of the subspeciation of hybrid types possessing any combination of the characteristics of the two species; such events must have occurred often during the species diversification of woodpeckers. However, this is not likely to occur to any perceptible extent, owing to the migratory habits of the birds and the absence of effective geographical barriers. Moreover, none of the various plumage characteristics appear to offer any particular advantage either as protective coloration or in sexual selection. Indeed, the evidence would indicate that hybrids possess an advantage, at least with the red-shafted species, probably due to the increased vigor that usually accompanies hybridity.

ALAN DEAKIN

CENTRAL EXPERIMENTAL FARM,
OTTAWA, ONTARIO

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WATER ABSORPTION BY REPTILE EGGS DURING INCUBATION

COMPARATIVELY little emphasis is laid upon the fact that for any evolutionary scheme which involves the origin of land vertebrates from aquatic forms the evolution of the egg is just as essential as the evolution of the adult and that the same general adaptations are requisite.

Two of the most important modifications necessary for the transition from water habitat to land habitat, in both adult and embryo, are (1) the conservation of moisture within the body and (2) the production of a respiratory system capable of securing oxygen directly from the atmosphere rather than from the air which is present in water.

It is to the former of these two problems that the present work is devoted. The common frog egg, which represents well the aquatic vertebrate type, during incubation not only retains its original moisture, but actually absorbs water from its environment. This may amount in some cases to as much as about 20 per cent. (based on weight increase) by the time of gastrulation. On the other hand, the hen egg, which may be used as an example of a terrestrial egg, does not absorb moisture from its environment during incubation, but on the contrary is forced to give up some of that originally placed within the egg; in our own experiments the loss of weight during normal conditions amounting by the tenth day of incubation to approximately 5 per cent. of the total weight of the egg.

Since the reptile lies in the proposed line of evolution from amphibia to birds, it should be worth while to investigate the eggs of some representatives of this class of vertebrates to determine whether there is absorption or loss of water during development. Several years ago the senior author (Cunningham, 1923) made a few observations on the eggs of the painted turtle *Chrysemys cinerea;* and Needham (1931) more recently used these as a part of his theory of the origin of terrestrial eggs.

The interpretation of Needham did not agree with that of the author, and further work was stimulated. *Chrysemys cinerea* has not been easily available, and the work reported here was carried out on the diamond back turtle *Malaclemys centrata* Lat. by the senior author, and on the fence lizard, *Sceloporus undulatus* Lat., by the junior author.

In the study of the lizard egg it has been assumed that the bulk of the loss or gain in weight of an egg is due to the change in water content, although Karashima (1929) states that in the marine turtle *Thalassochelys corticata,* along with an increase in the water content, there is also an increase in mineral and organic content. While his reported increase of the latter is more or less proportionate to the water intake the actual increase in mineral and carbohydrates, if it should occur, is for the

purpose of this study negligible. It is our intention, however, to make a more complete study of those relationships at a later time..

Uterine eggs of the fence lizard were taken, weighed, measured and placed under incubation conditions at ordinary room temperatures. From time to time each egg was reweighed and remeasured, the length and diameter being carefully determined. One hundred and twenty-four eggs from fourteen clutches were thus studied. Some of the eggs, probably because the shells were not properly developed or because of too much moisture in the incubating chambers, developed mould. However, 71 began to develop normally. Some half dozen died early in development. Of the remaining, 18 were carried through to hatching, while the others were opened at intervals to determine the relative stage of development.

The average weight of the 71 eggs when placed under incubation was 0.419 g. with a maximum of 0.500 g. and a minimum of 0.336 g. There was a steady increase in weight and on the 32nd day of incubation the 60 eggs remaining of these 71 averaged 0.794 g. with a maximum of 1.036 g. and a minimum of 0.602 g. The maximum average (0.912 g.) was reached on the 40th day of incubation; after this there was a rapid decline until hatching, which occurred between the 48th and 55th days of incubation. It is evident from these data that, on an average, the egg increases in weight more than 100 per cent. during incubation.

It may be urged that a part of this apparent increase in average weight might be due to the removal of lighter eggs for the examination of the embryos. On the contrary, eggs were taken at random, and the minimum weight of the 60 remaining eggs on the 32nd day was 20 per cent. greater than the maximum weight for any one egg at the beginning of the experiment. Furthermore, when the data for the 18 eggs which were carried to hatching are segregated one finds that from an original average weight of 0.465 g. the eggs attained an average of 0.948 g. on the 36th day of incubation, or an increase of more than 100 per cent. It should be pointed out that eggs increasing less than 50 per cent. of the original weight did not go far in development.

Since the pine lizard is typically terrestrial, these findings make a reexamination of the eggs of some such animal as the painted turtle imperative. Such study has already been begun

upon the eggs of *Chrysemys picta* and *Terrapena carolina,* but is not sufficiently advanced for report.

The senior author, through the courtesy of the U. S. Bureau of Fisheries, has for several summers studied the increase in weight of the eggs of the diamond back turtle at the Beaufort Laboratory. As in the case of the pine lizard the total increase in weight only has been considered, no effort thus far having been made to determine whether or not there is an increase in the mineral or carbohydrate content.

In the summer of 1934, 41 newly laid eggs of the diamond back turtle were taken from the nests and placed under artificial incubation conditions. Weights were taken on the first, third, fifth and the sixtieth or sixty-second days of incubation. Of the eggs set, 25 developed up to the time of closing the experiment (60–62 days), while most of those not progressing thus far (11) died before the third day of incubation. At the close of the experiment 25 of the eggs contained live embryos. These eggs had increased from an average of 9.945 g. at setting to 9.971 g. on the third day of incubation, and to 13.616 g. at 60 or 62 days, when the experiment was closed. This increase of 37 per cent. may not represent the maximum, since the eggs of this species usually hatch at about 65 days, and there may be a rapid loss in weight for several days before hatching, as in the case in the pine lizard. In the summer of 1935 some 18 eggs were set. Of these, eight were carried through 54 days of incubation. They increased from an original average weight of 10.176 g. to a final of 14.990 g. or about 47 per cent.

From the foregoing data it is quite evident that the diamond back turtle egg does increase in weight during development.

While the number of eggs in the following experiment is too small, if considered alone, to furnish conclusive evidence of water absorption by loggerhead turtle eggs the following data do add to the general concept that marine turtle eggs absorb considerable quantities of water, thus supporting the observations of Karashima.

Half a dozen eggs of the loggerhead turtle *Caretta caretta* were secured about a week after they were laid. One was immediately desiccated to determine the dry content for comparison with that found in the other eggs which were incubated for nearly two months. The average increase in weight of four of these eggs

which continued to develop was approximately 50 per cent. Further studies are to be made of the eggs of this turtle.

There is also during incubation an increase in the size of the fence lizard and diamond back turtle eggs. The increase in the former was recorded by Brimley (1903), and a similar occurrence was noted in Tuatera egg by Dendy (1898). The eighteen lizard eggs which were carried through to hatching were measured at setting and at the time they reached the maximum size and weight. While the eggs averaged an increase in volume of 0.449 cc, the average weight increase was 0.497 g. Eight diamond back eggs studied in the same manner gave an average volume increase of 3.143 cc, with an average weight increase of 4.812 g. Although there is no apparent ratio between volume and weight increase, in every case the latter was appreciably larger than the former.

From the work of Karashima (1929) it seems reasonable to suppose that the greater part of the increase in weight is due to water absorption, and experiments of our own indicate that the entire increase in weight can be accounted for by water absorption.

Four newly laid eggs of the diamond back turtle were desiccated to constant weight at 95° C. They were found to contain about 68 per cent. water and 32 per cent. solids. The proportion of water is less than that of the hen egg, in which the water varies from about 72 to 77 per cent., according to various authors (Needham, pp. 240–241).

The original dry weight of eight other diamond back eggs, calculated on this basis (*i.e.*, 68 per cent.), was found to average 3.31 g. per egg. After incubating for 54 days these eggs were desiccated at 95° C. for 48 hours and the average dry weight was found to be 2.83 g. per egg.

Since there is a loss in total solids, which is contrary to the findings of Karashima for the marine turtle, and since this loss occurs in every specimen tested, one may well conclude that the increase in weight represents the minimum of water absorbed by these eggs.

These experiments indicate the desirability of further investigation. Of the animals studied two are typically aquatic, the other typically terrestrial. The eggs of the terrestrial animal absorb much more water per unit weight than do the eggs of the aquatic ones; and this in spite of the fact that the eggs of

the latter are laid in what might be considered a "wetter" environment than the former.

BERT CUNNINGHAM
ARNOLD P. HURWITZ

DUKE UNIVERSITY

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HETEROGONY IN THE AXIAL SKELETON OF THE CREEPER FOWL

LANDAUER (1934) has recently published data on the skeletal growth of Creeper chickens. His analysis of the development of extremities of birds carrying the Creeper factor led him to conclude that certain deviations from the normal growth rhythm and growth intensity present in this stock are secondary to a general growth retardation. Furthermore, he concluded that these deviations are due both to changes in onset and in the rate of formation of the extremities. This analysis of the rate of growth of the bones of the axial skeleton was based on the calculation of the increments of growth from day to day in the embryonic period and from week to week in the post-hatching period as well as on calculation of the instantaneous percentage rate of growth.

The writer, in the course of a study of heterogonic growth in the posterior limb of normal fowls, has found that a definite distal-proximal gradient exists in the leg of chickens after hatching time. The detailed data of Landauer, presented in an appendix to his publication, afforded an opportunity to determine the existence of the same gradient in the embryonic period. Concurrently, it was possible to determine the heterogony constants for the Creeper chickens. The results of these calculations tend to throw additional light on the results obtained by Landauer and are deemed of sufficient interest to be presented here.

The general subject of heterogonic growth in relation to this and certain other types of problems is dealt with in detail in a study to be published by the writer elsewhere. It may be sufficient to point out here that the equation

$$y = bx^k \quad \text{.....(1)}$$

where y stands for a part and x for the whole, while b and k are heterogony constants, finds a wide application in the study of the rate of growth of a part in relation to the whole. It can be used with equivalent dimensions on the two sides of the equation or, as is the case here, with a mass (body weight) against a linear measurement (bone length). In the latter case, the k value does not represent the true differential rate, but needs to be corrected by the factor of three. When a number of observational points fall into a straight line on a double log plot of the part on the whole, a least squares fit can be obtained, giving a logarithmic regression line and yielding a solution for k in terms of y and x (Feldstein and Hersh, 1935)

$$k = \frac{n \Sigma \log x \log y - \Sigma \log x \Sigma \log y}{n \Sigma \log^2 x - (\Sigma \log x)^2} \quad \text{.....(2)}$$

The value of $\log b$ can be obtained by substituting k in one of the normal equations

$$\log b = \frac{\Sigma \log y - k \Sigma \log x}{n} \quad \text{.....(3)}$$

The standard error of k is given by Feldstein and Hersh (1935a) in the form

$$SE_k = \sqrt{\frac{n \Sigma \log^2 y - (\Sigma \log y)^2}{n \Sigma \log^2 x - (\Sigma \log x)^2} - k^2} \quad \text{.....(4)}$$

However, the standard error of $\log b$ has not been heretofore presented in literature on heterogonic growth. It may be derived through the following transformation of the formula of Working and Hotelling (Ezekiel, 1930, p. 254). Some of the terminology of Ezekiel has been changed to conform to that used by workers in heterogonic growth.

The standard error of the estimated value of $\log y$ (y^1) is

$$\sigma_{y1} = \sqrt{\sigma_{M_y}^2 {}^1 + \sigma_{k \log y \log x}^2 (\log x - \overline{\log x})^2} \quad \text{.....(5)}$$

From

$$y = bx^k \quad \text{.....(1)}$$

$$\log y = \log b + k \log x \quad \text{.....(6)}$$

Hence $\log b$ is the value of $\log y$ when $\log x = 0$. Then the expres-

sion $(\log x - \overline{\log x})^2$ is equal to the square of the mean $\log x$. Further,

$$\sigma_{xy}1 = \frac{\overline{S}_{\log y \log x}}{\sqrt{n}} \quad \ldots\ldots(7)$$

and

$$\sigma k_{\log y \log x} = \frac{\overline{S}_{\log y \log x}}{\sigma_{\log x}\sqrt{n}} \quad \ldots\ldots(8)$$

where

$$\overline{S}_{\log y \log x} = \sqrt{\frac{n\sigma^2 z}{n-2}} \quad \ldots\ldots(9)$$

Here z represents the excess of the observed over the estimated value of $\log y$ for each $\log x$.

σ_z can be obviously calculated from

$$\sqrt{\frac{\Sigma z^2}{n}} \quad \ldots\ldots(10)$$

while

$$\sigma_{\log x} = \sqrt{\frac{n\Sigma \log^2 x - (\Sigma \log x)^2}{n^2}} \quad \ldots\ldots(11)$$

By substitution

$$SE_{\log b} = \sqrt{\frac{\Sigma z^2}{n(n-2)}} \sqrt{1 + \frac{n^2 \overline{(\log x)^2}}{n\Sigma \log^2 x - (\Sigma \log x)^2}} \quad \ldots\ldots(12)$$

In preparing a plot of the growth of the limbs of the embryo chick, it was found that a change in intercept occurs between the eighth and ninth day of incubation. The period used for determination of the heterogony constants was consequently selected within the limits of nine and twenty-one days.

Table 1 presents firstly the values of k for the normal and the Creeper chicks. It may be observed that in light of the respective standard errors the two groups of chicks show no difference in k for any of the six bones studied. This can be interpreted to mean that no retardation in the rate of growth of any of the bones with respect to the growth of the whole body within the limits of the period of study can be noted.

However, $\log b$, which is also shown in Table 1, has significantly higher values of the normal over those of the Creeper chicks. The interpretation of this difference has to be approached very carefully. Since the value of $\log b$ has been arrived at by extrapolation it does not necessarily represent the actual value of $\log y$, when $\log x = 0$, this point being absent from the data. The change in intercept observed between the eighth and ninth days of incubation will necessarily invalidate $\log b$ as an absolute measure.

TABLE 1
HETEROGONY CONSTANTS OF NORMAL AND CREEPER EMBRYOS

	k		$\log b$		
	Normal	Creeper	Normal	Creeper	Ratio
Femur	0.539 ± 0.055	0.534 ± 0.045	0.523 ± 0.014	0.450 ± 0.013	0.86
Tibiotarsus	0.571 ± 0.063	0.598 ± 0.055	0.626 ± 0.022	0.468 ± 0.019	0.75
Tarsometatarsus	0.603 ± 0.045	0.627 ± 0.071	0.460 ± 0.014	0.305 ± 0.021	0.66
Humerus	0.484 ± 0.045	0.508 ± 0.045	0.469 ± 0.011	0.360 ± 0.016	0.77
Ulna	0.466 ± 0.045	0.488 ± 0.055	0.453 ± 0.011	0.325 ± 0.016	0.72
Radius	0.479 ± 0.032	0.488 ± 0.045	0.404 ± 0.016	0.281 ± 0.016	0.70

It can, however, be readily interpreted to mean that a retardation in the growth of the limbs of the Creeper took place at a stage of embryonic development earlier than nine days. On the face of the fact that the k values are the same in the Creeper and the normal embryos, this retardation may be assigned to a differential onset of limb formation. Such conclusion may, however, be dangerous, since the k values preceding the ninth day of incubation may be also different. It is obvious, however, that while the effect of retardation is general it can be observed to a greater extent on the limb bones than on the whole body, since otherwise heterogony constants calculated on the basis of body weight would not reveal any differences between normal and Creeper fowls.

Table 1 also presents the ratio of $\log b$ of the Creeper to $\log b$ of the normal birds and here it may be seen that the gradation is proximal-distal. This would indicate that the greatest reduction in length with respect to body weight took place in bones laid down the latest, presenting a confirmation of Landauer's analysis by an entirely different method. It may also be mentioned that the growth gradient in k value can be observed here in both the Creeper and the normal embryos, thus duplicating the writer's findings for the post-hatching period of growth in normal stock.

I. MICHAEL LERNER

POULTRY DIVISION
UNIVERSITY OF CALIFORNIA, BERKELEY

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